

AN  
INTRODUCTION  
TO  
NEMATOTOLOGY

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Babylon, N. Y.

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1859-1932

Born in Spencer, Mass.; B. Sc. Worcester Polytechnic Institute (1881); Instructor in chemistry and natural history at Williston Seminary, Easthampton, Mass. (1881-1887); Ph. D. University of Jena (1888); Investigator at Naples Zoological Station (1888); commercial advertiser at Sydney, N. S. Wales (1889); temporary professor of zoology in University of Sydney (1889-1890); pathologist, Department of Agriculture, N. S. Wales (1891-1901); special commissioner on Agriculture for N. S. Wales, visiting Europe and United States (1901-1904); director, Division of Physiology and Pathology, Hawaiian Sugar Planters' Experiment Station (1905-1906); Agricultural Technologist, U. S. Department of Agriculture (1907-1928); Principal Nematologist, U. S. Department of Agriculture (1929-1932).

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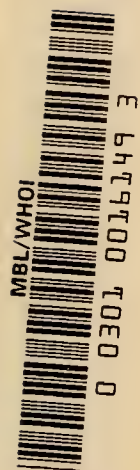
## PREFACE

THE authors wish to express their appreciation to the various workers and institutions which supported the first part. Such support, even in so limited a field, will assure completion of the series.

This part, covering as it does, the digestive tract and associated structures, includes most of the characters commonly used in identification. In order to give as comprehensive a survey as possible many of the illustrations are semidiagrammatic (those not shaded). In all cases they are based on camera lucida sketches. The side view series of diagrams may be assumed to have the dorsal side at the readers left unless otherwise specified.

The authors wish to express their appreciation to Doctor G. Steiner, Doctor J. R. Christie and Miss E. M. Buhner, all of the Division of Nematology, U. S. Bureau of Plant Industry, for their helpful criticism.

B. G. C. & M. B. C.





## CHAPTER V

### CEPHALIC STRUCTURES AND STOMA

The various structures which go to make up the cephalic region of nematodes cannot be classified in a single category. Yet their study is naturally interlocked both in practical and developmental anatomy. Under the general heading "Cephalic structures" we shall discuss lips, pseudolabia, cephalic papillae, cephalic setae, amphids, probolae, collarettes, cordons and labial dentition while under the heading "Stoma" that part of the digestive tract between the oral opening and the anterior end of the esophagus will be considered. Of necessity, a discussion of cephalic structures must include parts of the nervous system, external cuticle and sometimes stomatal developments. Likewise, a discussion of the stoma overlaps to some extent both with the cephalic structures and the esophagus.

#### 1. CEPHALIC STRUCTURES

Cephalic structures have been used, to a limited extent, as taxonomic characters since the appearance of Schneider's monograph (1866) which included *en face*, as well as lateral and medial views of the anterior extremity of many of the larger nematodes. Such studies were extended by de Man (1886-1907) investigating free-living nemas and von Drasche (1883) working with parasitic nemas of Diesing and Molin's collections. Certain generalities came to be accepted as a result of the observations of Schneider and von Drasche. These were as follows: (1) That ascarids and heterakids have three lips, one dorsal and two subventral; (2) That spirurids have two lateral "lips" and (3) That parasitic nemas generally have four submedian and two lateral cephalic papillae. The first two of these points are for the most part acceptable to us today but the third is no longer tenable. In parasitic nemas Looss (1902) introduced the use of cephalic structures in strongylid taxonomy causing them to be considered an integral part of generic and specific descriptions in this group but, apparently due to lack of interest or inadequacy of parasitological technique, little advance was made beyond Schneider, von Drasche, and Looss until very recently. In free-living nemas somewhat more steady progress has been made, partially attributable to the smaller size which makes critical study convenient and partially due to more widespread technical training. Though numerous workers have contributed to our knowledge of free living nemas, the chief impetus has come from the work of Cobb and Steiner. The glycerin jelly technique (see Cobb, 1920, and Chitwood and Wehr, 1934) developed in the laboratory under Cobb was introduced to the various visitors and associates; this technique made the study of nemas from *en face* practical.

Knowledge of the basic anatomy of the anterior end is due to the contributions of Goldschmidt (1903), Martini (1916), and Höeppli (1925). The confusion of two types of sensory organs, tactile structures (papillae) and chemoreceptors (amphids) in parasitic nemas caused much misunderstanding though Goldschmidt recognized the difference between the dorsal lateral organ (amphid) of *Ascaris lumbricoides* and the other sensory organs. The same differences both in the terminal sensilla and the internal nervous connection were brought out by Zur Strassen (1904), Looss (1905), and Martini (1916) in *Siphonolaimus* spp., *Ancylostoma duodenale* and *Oxyuris equi*, respectively. Zur Strassen even went so far as to state definitely that the dorsal lateral organ of *Ascaris* is the same as the circular lateral organ of *Siphonolaimus*. Other workers entirely ignored these observations until Cobb (1913) renamed the lateral organs *amphids* defining them as paired cephalic structures of specialized (unknown) function. It remained for the same author later (1923, 1924, 1928) to establish the general existence of pore like amphids in parasitic nemas through observation and constant reiteration that they are not "lateral papillae." Since then information has gradually accumulated showing their universal presence in the Nematoda. We shall not go into their internal anatomy at the present time since they are connected with the nervous system. It will be sufficient to note that each amphid is essentially a lateral or dorsolateral organ connected internally with the *lateroventral* commissure and with a gland (Fig. 3). Near the external orifice there is a dilation of the gland duct (amphidial pouch) in which nerve fibers terminate (the sensilla) (Fig. 8); the pouch is connected with the exterior either directly by an amphidial tube and pore or it opens into a pocket, circle or spiral external cuticular modification. In this part, only the external manifestation of the amphid (i. e., pore, pocket, spiral, etc.) will be considered.

In 1918 Filipjev introduced the external form of the amphids of free-living nemas as a family and subfamily character, later (1929, 1934 a, b) raising its use to suborders.

In the meantime information regarding the number and arrangement of cephalic sensory organs in both parasitic and free-living nemas was accumulating and Chitwood and Wehr (1932, 1934) brought out papers on the evolution and basic plan of cephalic structures with special reference to parasites while Stekhoven and de Coninck (1933), de Coninck (1935) and Stekhoven (1937) brought out similar papers with special reference to free living nemas. Differences in findings are for the most part matters of interpretation due to opposed schools of thought; the differences being in basic philosophy as to the evolution of nemas and not in the organisms themselves. The one school, represented by Filipjev, Stekhoven, and de Coninck regard polymyarian nemas as primitive and meromyarian nemas as neotenic while the other school, represented by Looss, Steiner and the writers, consider meromyarian nemas as primitive and polymyarian nemas as more highly evolved. The consequences are that each group sees the Nematoda from a separate point of vantage.

The basic plan of the anterior end appears to be six lips, two subdorsal, two lateral, and two subventral. On the summit of each lip there is a papilla, these six papillae constituting the internal circle and being known as internodorsals (id), internolaterals (il), and internoventrals (iv); situated more posteriorly on each of the submedian lips there are two papillae while on each of the lateral lips there is one papillae; these papillae constitute the external circle and have been named according to their position (Fig. 8a): dorsodorsals (dd), laterodorsals (ld), ventrolaterals (vl) (or externolaterals, el), lateroventrals (lv) and ventroventrals (vv). All of the members of the external circle are seldom exactly the same size or at exactly the same level. Stekhoven and de Coninck (1933) would therefore speak of them as constituting two circles and in some forms this is indeed the case. However, the papillae of the external circle are not always segregated in the same pattern. Thus the ventrolateral papillae tend to agree with the dorsodorsal and ventroventral papillae in their relative development in the Aphasmidia while they tend to agree with the laterodorsal and lateroventral papillae in the Rhabditina, Strongylina and Ascaridoidea. For that reason we regard the external circle as subdivisible into two papillary groups.

Fusion and reduction of cephalic papillae commonly modify the apparent cephalic arrangement but one can practically always recognize remnants of the original papillae and all cases may be explained in terms of the diagram presented (Fig. 8A).

As pointed out by Chitwood (1932) and the writers (1933) the cephalic papillary nerves are hexaradiately symmetrical and one would expect a hexaradiate symmetry to be basic for the papillae. Therefore, the external circle should consist of 12 papillae instead of 10. However, no rudiments of a dorsolateral pair are known except in some species of the Monhysteridae and Linhomoeidae. If these forms were the more primitive, one would expect to find rudiments of the aforementioned papillae in other groups and this is not the case.

The bilaterally symmetrical amphids are separately innervated and cannot be considered a part of the cephalic papillary symmetry. Unlike the papillary nerves, the amphidial nerves enter the nerve ring indirectly, through a commissure and their original position probably was posterior to the labial region as indicated by embryonic rhabditids and adult aphasmidians. Likewise, the amphidial orifice was probably larger and a bit like the plectoid amphid, if one is to interpret on the basis of embryonic rhabditids. As pointed out by the writers (1933) one cannot assume any existing form to represent the protonematode but if one combines characters of the genera *Rhabditis* and *Plectus* a common denominator of all nematodes is found. One cannot interpret aphasmidians entirely in terms of *Rhabditis* nor phasmidians in terms of *Plectus*, but the converse is moderately natural. Thus the amphids and papillae are basically labial in position in phasmidians while the amphids in aphasmidians are basically postlabial (a more primitive arrangement) and some of the papillae may be postlabial in position (a less primitive arrangement).

Regarding the basic number of lips, there are two choices. One may assume primitive triradiate symmetry in accordance with the symmetry of the esophagus as did Baylis and Daubney (1926) or a hexaradiate symmetry in accordance with the



papillary arrangement as did the writers (1933). Since the lips are not formed from the esophageal primordium but from the cells of the anterior end (elavate cells of the papillary nerves and arende lobes) the esophagus has nothing to do with them. The clavate cells are hexaradiately symmetrical while the arcade is bilaterally symmetrical with a gross triradiate and an actual 9-radiate symmetry (Fig. 46B). The actual 9-radiate symmetry is subdivisible into a triradiate and a hexaradiate formation rather than into three triradiate systems. We shall assume a hexaradiate symmetry as basic. Taking either extreme, six distinct lips or three distinct lips one finds repetitive series of transitions from the one to the other in the large groups. The lips themselves are subdivisible into two portions, the *apical part*, bearing the internal circle of papillae and the *basal part*, bearing the external circle of papillae and amphids in the Phasmidia and at least one subdivision of the external circle in the Aphasmidia. In some instances the two parts of a lip may be represented by separate lobes as in *Spironoura affine* and *Parascaris equorum* (Fig. 57) while in other instances, *Oxyuris equi*, *Metoncholaimus pristiurus* (Figs. 57 and 63) only the apical lobes may persist.

Original lips may totally disappear and be replaced by newly formed structures such as the pseudolabia of spinroids, the probolae of cephalobids and the pseudonchia of filarids.

In the study of cephalic structures the student should be quite critical. It is not uncommon for two workers examining the same species to find greater differences than one worker would find examining representatives of two families. Lateral and medial views are often quite helpful but without an en face view they may be meaningless. It is due to this fact that the majority of older descriptions of the cephalic structures of parasitic nemas must be considered valueless. In examining en face views great care should be taken in focusing the microscope, and oil immersion is essential even in the study of the largest species.

## A. PHASMIDIA

Phasmidians are similar to one another in the possession of simple external amphids, usually pore like and labial in position. The cephalic sensory organs are nearly always papilliform and in the most extreme cases are no more than setose papillae. In cases of reduction or fusion of the external circle it is always the dorsodorsals and ventroventrals that tend to disappear. The physiognomy of the various members of the subelass will be dealt with systematically.

**RHABDITINA.** Members of the suborder Rhabditina (Figs. 54-55) characteristically have six lips but three-lipped forms are quite common and many genera have no lips. The cephalic papillary arrangement is likewise diverse.

**Rhabditidae.**—Both six and three-lipped forms are common in the Rhabditidae and one finds every conceivable variation between the two. In *Rhabditis terricola* there are six large separate lips, an internal circle of six well developed papillae and an external circle of ten well developed papillae; the latter are not absolutely equal in form or size, the dorsodorsals and ventroventrals being similar as are the laterodorsals and lateroventrals while the ventrolaterals are more or less intermediate between the others. *Rhabditis lucanii* has three basally bilobed lips and the same number and arrangement of papillae but in this instance the ventrolaterals are small and like the dorsodorsals and ventroventrals. Other rhabditids vary between these types some having discrete, some confluent lips; in some the labial region is set off from the remainder of the body while in others this is not the case. In all instances the amphids are dorsolateral and labial in position and pore-like in character.

In *Diploscapter coronata* the lips have been entirely transformed into a pair of medial, outwardly acting, distally bifurcate fossorae and a pair of lateral lamellae. Neither papillae nor amphids have been satisfactorily studied.

**Cylindrogasterids** have six discrete lips which may or may not be set off from the remainder of the body; there is an internal circle of six reduced papillae. In *Longibucca vivipara* and *L. lasiura* there is an external circle of four well developed papillae (laterodorsals and lateroventrals) and in the latter ventrolaterals are also present but reduced. In *Cylindrogaster longistoma* there are six well developed (ld., vd., and lv.) and four reduced (dd. and vv.) papillae. The amphids are dorsolateral and labial in all forms.

In the family Diplogasteridae the two chief groups based upon the esophagus, Alloionematinae and Diplogasterinae, seem to differ also in cephalic characters. Members of the Alloionematinae usually have rather distinct lips, six (*Alloionema appendiculatum* v. *dubium*) or four (*Cheilobus quadrilabius*); in the latter instance the submedial lips are

fused; only six papillae have been observed, these presumably being the laterodorsal, lateroventral and ventrolaterals. Alloionematids have pore like, labial, dorsolateral amphids and a simple hexagonal oral opening. The closely related family Strongyloidiidae is characterized by two lateral lips, this being practically the only character distinguishing the free-living generation from such genera as *Alloionema* and *Rhabditophanes*. Diplogasterids usually have no lips (*Diplogaster fector*, *Mononchooides americanus* (Syn. *Diplogaster americanus*)) but instead they have a thin circum-oral membrane supported by longitudinal rugae which project anteriorly from the stoma. The number and degree of development of the rugae differs in the various species. In other genera inconspicuous remnants of six lips may be present (*Pristionchus*, *Rhabditoides*, *Odontopharynx*). Among the forms thus far studied, *Pristionchus acrivora* is the only one known to show the full complement of papillae (16); in this instance the dorsodorsal and ventroventral papillae are reduced while the others are well developed. In all other members of this subfamily studied the internal circle and the externomedial papillae are rudimentary or apparently absent. The remaining six papillae are often conically setose. Another peculiarity of the group is that the amphids vary from pore like and labial in position to slit or transversely elliptical (with similarities to *Plectus*).

The family Cephalobidae contains forms with six lips (*Panagrolaimus subelongatus*), three lips (*Cephalobus persegnis*, *Tricephalobus longicaudatus*) three simple (*Acrobeloides bütschlii*) or bifid labial probolae and sometimes six cephalic probolae (*Acrobeles complexus*). Labial probolae are cuticular labial structures which apparently replace the lips. They may be recognized by the fact that they are separated from the papillae bearing labial rudiments by a groove; cephalic probolae are known to occur only coincidentally with labial probolae, project anteriorly and often bear the cephalic papillae at their bases (*Acrobeles bodenheimeri*). Lips, on the contrary, bear papillae close to their apices. Another representative of this odd group (*Chambersiella rodens*) possesses six inwardly acting *odontia* internal to which there are six cirri (? cephalic probolae). When lips are present the full complement of cephalic papillae (16) are often observable but in other instances they become difficult to recognize.

Of the remaining families of the Rhabditoidea the Steinerematidae (*Neoplectana glaseri*) have a rounded oral opening, no lips, and the full complement of well developed papillae and the Angiostomatidae (*Angiostoma plectodontis*) have three inconspicuous lips and the full complement of papillae while the Drilonematidae are devoid of lips and have only the external circle of papillae, eight in *Dicelis nira* and four in *Ungella secta*. Drilonematids may also have large hook-like teeth projecting from the stoma (*Ungella secta*).

Representatives of the Tylenchoidea have not been sufficiently studied to make many statements regarding their cephalic characters. As a rule the labial region is distinct, the lips inconspicuous, six in number, and bearing four papillae and the amphids. In a few forms such as *Anguina tritici* and *Rotylenchus similis* an internal circle of six papillae have been observed, these papillae being internal to the lips. In some tylenchids such as *Hoplolaimus bradys* the labial region is striated and supported by a sclerotized framework. In at least one form (*Neotylenchus abulbosus*) there is a medial pair of supplementary lips between the original six lips.

**STRONGYLOINA.** *Strongyloidea.*—The majority of representatives of the superfamily Strongyloidea have no lips or they are greatly reduced or rudimentary. In all instances the amphids are dorsolateral or lateral and labial in position.

In the family Strongyliidae lips are absent and in their place one finds the *external corona radiata* or leaf crown (Fig. 56). As we interpret these structures, they represent the divided apical lobes of the original lips; they may number from six to 40 or more. The labial region is generally set off from the remainder of the body by a groove but it is not divided longitudinally as when large lips are present. Within this family the internal circle is usually rudimentary or apparently absent but it may be represented by reduced internolaterals (*Strongylus equinus*). The external circle is represented by four large, often setose, submedian papillae each of which apparently consists of two original papillae that have fused (dd.—ld. and vv.—lv.); ventrolaterals are rudimentary.

The closely related family Syngamidae supplies interesting examples for comparison with the Strongyliidae. In *Stephanurus dentatus* and *Syngamus trachea* the oral opening is subhexagonal or one might say there are six rudimentary lips while in *Delectrocephalus demidiatus* there are six distinct lobes which might equally well be termed an external corona radiata or rudimentary labial lobes. In all three forms the internal circle is reduced but, nevertheless, distinct and the external

circle consists of ten papillae. There is a distinct tendency toward fusion of papillae with coincident reduction in size of the dorsodorsals, ventrolaterals and ventroventrals the median pairs of the external circle being nearly completely fused in *Stephanurus dentatus*, partially fused in *Syngamus trachea* and separate but approaching in pairs in *Deiletocephalus demidiatus*. As in the Strongylidae the labial region is usually set off by a groove but unlike the Strongylidae, the medial papillae of the external circle are never in the form of duplex setose papillae (Fig. 56).

The family Ancylostomatidae is characterized by the absence of both lips and a corona radiata; instead the oral opening is modified to the function of prostomatal teeth or cutting edges. As exemplified by *Necator americanus* the full component of papillae are represented, all of them being reduced with the exception of the laterodorsals and lateroventrals and one finds the medial pairs of the external circle closely approximate as in the Syngamidae. The labial region is not set off by a groove as in the previously mentioned families.

The family Diaphanocephalidae is characterized by a dor-

soventrally elongate oral opening and is without lips, leaf crown, prostomatal teeth or cutting edges. The full component of papillae is represented, there being an internal circle of six reduced papillae and an external circle of four incompletely fused submedial and two simple ventrolateral (*Kali cephalus* sp.).

The family Cloacinidae is particularly noteworthy because of the presence of six massive lips, the laterals somewhat lower than the submedians. In *Zoniolaima setifera* the internal circle is represented by reduced internolaterals and the external circle by four (? duplex) conoid papillae.

*Trichostrongyloidea*. Representatives of this superfamily often have a distinct cephalic inflation or cuticular helmets of numerous specialized forms which are used as generic characters. They are always devoid of a leaf crown and seldom show rudiments of either six or three lips. The oral opening may be of diverse form but is nearly always surrounded by an inconspicuous circumoral membrane. Representatives studied by the writers have an internal circle of six reduced papillae and an external circle of 10 simple papillae (medials

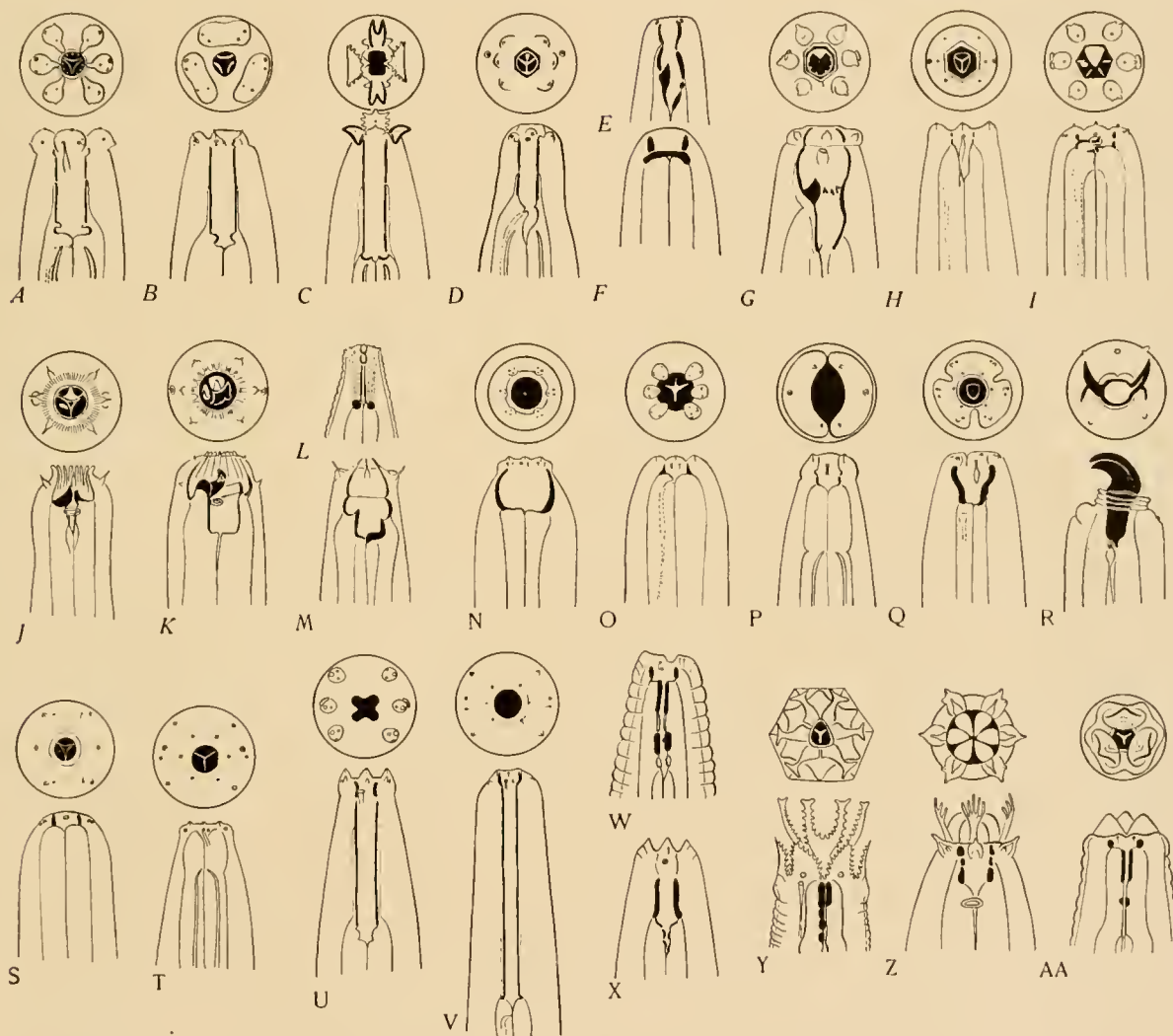


FIG. 54.

Cephalic regions in the Rhabditoidea. A-C—Rhabditidae, D-M—Diplogasteridae, N-O—Rhabdiasidae, P—Strongyloidea, Q—Angiostomatidae, R-S—Drilonematidae, T—Steinernematidae, U-V—Cyndrogasteridae, W-AA—Cephalobidae. A—*Rhabditis terricola*; B—*Rhabditis aspera*; C—*Diploscapter coronata*; D—*Rhabditoides* sp.; E—*Acrostichus toledoi*; F—*Lycolaimus iheringi*; G—*Odontopharynx longicaudatus*; H—*Alloinaena appendiculatum* v. *dubia*; I—*Pristionchus aerivora*; J—*Diplogaster fector*; K—*Mononchoides americanus*; L—*Tylopharynx striata*; M—*Butlerius butleri*; N—*Entomelas entomelas*; O—*Rhabdias eustreptos*; P—*Strongyloides ransomi*; Q—*Angiostoma plethodontis*; R—*Ungella seta*; S—*Dicelis nira*; T—*Neoplectana glaseri*; U—*Cylindrogaster*; V—*Longibucca laxiura*; W—*Cephalobus persequens*; X—*Panagrolaimus sublongatus*; Y—*Aerobes camplesus*; Z—*Chamberiella rodens*;

AA—*Aciroboides hutschlii*. E-F—After Rahm, 1929, Arch. Inst. Biol. v. 2. G—After de Man, 1912, Zool. Jahrb. Abt. Syst., v. 33(6). H—After Chitwood and McIntosh, 1934, Proc. Helm. Soc. Wash., v. 1(2). I—After Steiner, 1934, Proc. Helm. Soc. Wash., v. 1(2). L-M—After Goodey, 1929, J. Helminth., v. 7(1). P—After Alicata, 1935, U. S. D. A. Tech. Bull. 489. R—After Cobb, 1928, J. Wash. Acad. Sc., v. 18(7). S—After Chitwood and Lucker, 1934, Proc. Helm. Soc. Wash., v. 1(2). T—After Steiner, 1929, J. Wash. Acad. Sc., v. 19(19). U—After Steiner, 1933, J. Parasit., v. 20(1). V—After McIntosh and Chitwood, 1934, Parasit., v. 26(1). W-X—After Thorne, 1937, Proc. Helm. Soc. Wash., v. 4(1). Y and AA—After Thorne, 1925, Tr. Am. Micr. Soc., v. 44(4). Z—After Cobb, 1920, Contrib. Sc. Nemat. 9. Remainder original.



approaching in pairs), six medials partially or completely fused) or four (ventrolaterals apparently absent).

**Metastrongyloidea.** Members of this superfamily have neither the corona radiata of the Strongyloidea nor the cephalic inflation of the Trichostrongyloidea. Lips, if present, are much reduced except in *Metastrongylus* which has six massive lips, the largest of which are lateral. The oral opening is usually rounded and the labial rudiments, if present (*Filariopsis arator*, *Stenurus* sp.) set somewhat far back from the mouth and bear upon them only the internal circle of papillae. The same tendency of papillary reduction and fusion observed in the Strongyloidea and Trichostrongyloidea follows also in this superfamily, medials of the external circle being smaller as are also the ventrolaterals (*Filariopsis*, *Stenurus*, *Dictyocaulus*, *Metastrongylus*).

**ASCARIDINA.** Members of the Ascaridina usually have three lips, one dorsal and two subventral (Fig. 57). While the internal circle of papillae is always reduced or rudimentary the two superfamilies differ as regards the external circle. In the Oxyuroidea the ventrolateral papillae are always rudimentary or absent while in the Ascaridoidea these papillae are well developed.

**Oxyuroidea.** In this superfamily the Thelastomatidae appear to be most primitive as regards cephalic papillae, for the external circle consists of eight quite separate papillae practically equal in size (*Leidynema appendiculatum*, *Protrellina floridana*, *Aorurus philippinensis*). However, in this family lips are usually absent, there being a delicate circumoral membrane. In a few exceptional forms three reduced lips may be preserved (*Fontonema brachygaster*) and sometimes a lobing of the circumoral membrane may give the appearance of six reduced lips, two medial, four submedial (*Aorurus philippinensis*).

The family Oxyuridae appears to be a direct development of the Thelastomatidae in other structural characters but the fact that most members of this family retain three distinct lips (*Enterobius vermicularis*) and one form (*Oxyuris equi*) preserves the rudiments of six lips, seems to indicate that they must have originated rather early in thelastomatid phylogeny. Unlike thelastomatids, oxyurids have only four well developed papillae of the external circle. We interpret these as compound papillae formed by reduction of the mediomedials (dd. and vv.) and their complete fusion with the lateromedials (ld. and lv.). Secondary labial changes produce forms with two lateral lips by disappearance of the dorsal lip (*Maeracis monohystera*) and others with four lips by division of the dorsal lip (*Aspicularis tetraptera*). Perhaps the strangest case of labial

modification occurs between the closely related genera *Wellcomeia* and *Syphacia*. In the former genus there are the usual two subventral and one dorsal lip while in the latter genus there is one ventral and two subdorsal. This absolute reversal in symmetry of the lips is not accompanied by reversal in other organs; the dorsodorsal papillae of *Syphacia* are on the subdorsal lips, each of which has two compound papillae and an amphid in the usual symmetry; the ventral lip has no papillae.

The family Rhigonematidae is like the Oxyuridae in number of cephalic papillae and the subfamily Rhigonematinae contains forms with the common three lip symmetry (*Rhigonema infectum*). However, the other subfamily, Iethyocephalinae, presents a startling modification of symmetry. The head is divided forming two jaws and contrary to general opinion and to all other nematodes, the jaws are dorsal and ventral instead of lateral. The four compound papillae and lateral pore like amphids retain their normal positions not being modified by the change in symmetry.

Members of the Atractidae are the most diversified in cephalic characters of the whole suborder Ascaridina. Many of these forms are highly specialized and yet one must concede them a very ancient position in the Oxyuroidea very close to the Thelastomatidae. Like the oxyurids and rhigonematids they have only four compound papillae in the external circle and in this respect the thelastomatids should be more primitive. Six, three, and two lipped forms all occur in the Atractidae. The genus *Atractis* has six well developed lips not unlike *Rhabditis terricola*, while *Crossocephalus* has three lips like oxyurids. *Puleirocephala* retains the three lips but has in addition cuticular projections from the labial region which may take innumerable forms but each element is grossly similar to an insect wing. *Heth*, on the other hand, has two lateral lips with corrugated edges and is provided with a spinate cephalic collar, while in *Labidurus gulosus* the dorsal lip is replaced by a tuft like appendage. In the ransomnematomids (*Heth*, *Puleirocephala* etc.) the highly specialized or ornamental cephalic structures are confined to the female and do not make their appearance until the last molt.

**Ascaridoidea.** Members of the Ascaridoidea generally have three large conspicuous lips; the ventrolateral papillae and the other members of the external circle are all well developed. Throughout the entire group the medial pairs of the external circle are incompletely fused. One cannot assume ascaridoids, having the full complement of papillae, arose from oxyuroids but neither can one assume the reverse for the entirely sepa-

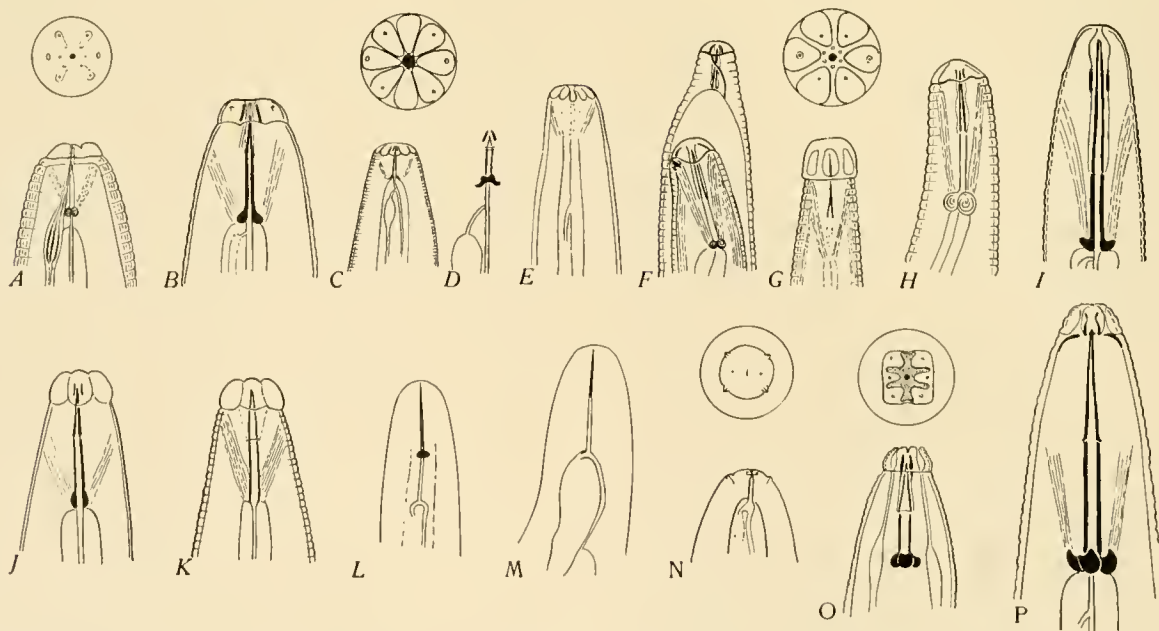


FIG. 55.

Cephalic region in the Tylenchoidea. A-K and O-P—Tylenchidae. M-N—Allantonematidae. A—*Anguina tritici*; B—*Ditylenchus dipsaci*; C-E—*Neotylenchus abulbosus* (C-D, female; E, male); F-H—*Rotylenchus similis* (F, female at last molt; G, upper, head of adult female and lower, adult male; H, adult female); I—*Paratylenchus macropallus*; J—*Aphelenchoides pacificus*; K—*Aphelenchus avenae*; L—*Heterotylenchus aberrans* (adult free-living female); M—*Allantonema mirabile* (adult free-living female); N—*Chondronema passali*;

O—*Hoplolaimus bradys*; P—*Rotylenchus robustus*. A—After Steiner, 1925, Phytopath., v. 15(9). C-D—After Steiner, 1931, J. Wash. Acad. Sc., v. 21(21). E—After Steiner and Buhner, 1932, J. Wash. Acad. Sc., v. 22(16). F-H—After Steiner and Buhner, 1933, Ztschr. Parasitenk., v. 5(2). I-M—After Bovie, 1937, Some types of association between nematodes and insects. N—After Christie and Chitwood, 1931, J. Wash. Acad. Sc., v. 21(15). O—After Steiner and Le Hew, 1933, Zool. Anz., v. 101(9-10). Remainder original.



rate median pairs of thelastomatids could hardly have arisen from any known ascaridoid.

In cephalic papillary arrangement ascaridoids show practically no diversity but in labial developments diversity is marked.

Members of the Cosmocercidae (*Cosmocercoides dukae*), Heterakinae (*Heterakis gallinae*) and Ascarididae (*Ascaris lumbricoides*) all have three large lips. In addition to the lips there may be posteriorly directed cuticular cordons (*Aspidodera* and *Heterocheilus*, Heterakinae and Anisakinae resp.) and between the lips there may be interlabia (*Porrocaecum* and *Parascaris*, Anisakinae and Ascaridinae resp.). The lips, themselves, may bear denticles on their internal surfaces (*Porrocaecum*, *Ascaris*); the apical lobes may be separated from the basal lobes by grooves (*Parascaris*); and the labial pulp may assume diverse forms which are considered specific (*Polydelphis quadricornis* and *P. boddaerti*). Members of the Subulurinae differ from other ascaridoids in that the lips are reduced to apical lobes bearing only the internal circle of papillae and there may be three (*Subulura distans*) six, or more apparent lobes. The grossly twelve lobed oral opening of *Aulonoccephalus peramelis* is interpreted as having rudiments of six lips (the apical lobes) separated by six interlabia. Within the Kathlanidae all manner of labial multiplicity is known, the genus *Spectatus* being characterized as having six lips, *Spirogonura* as having three lips, *Kathlania* with about 16 labial divisions and *Cissophylus* with a bilaterally symmetric head. Of these only *Spirogonura* and *Cissophylus* have been carefully studied. In *Spirogonura* the lips are essentially ascaroid with the apical lobes separated from the basal by grooves. In *Cissophylus roseus* the dorsal lip is reduced, and transformed into a three pronged odontium while the subventral lips are massive and dentate.

**CAMALLANINA.** The suborder Camallanina (Fig. 58) differs from the Rhabditina, Strongylina and Ascaridoidea in that ventrolateral papillae are entirely unknown. Well developed lips are never present but rudiments of lips or lateral jaws may occur.

**Cumallanoidea.** Most of the members of this superfamily have no lips but instead two lateral jaws. However, the genera *Omcia* and *Haplonema* (Cuenllanidae) as described by Hsü (1933) and the genus *Procamallanus* as described by Li (1935) preserve a less specialized condition. In *Omcia* six labial rudiments (apical lobes) are present, in *Haplonema* lips are absent and in *Procamallanus* the oral opening is hexagonal. The internal circle is in all instances reduced in size and the external circle represented by four papillae (duplex in Cuenllanidae and simple in Camallanidae).

**Draunculoidea.** Draunculoids are devoid of both lips and jaws, the rounded oral opening being surrounded by a very thin circumoral membrane external to which there may (*Draunculus*, *Aroiserpens*) or may not (*Philometra*, *Micropleura*) be a cuticularized circumoral elevation. The internal circle is well developed (a more primitive condition than in the Camallanoidea) and so also are the eight members of the external circle. In *Micropleura* and *Philometra* all of the papillae remain distinct while in *Draunculus* and *Aroiserpens* the medians of the external circle are partially fused. In *Draunculus* the internodorsals and internodorsals fuse in the development of the female while the male retains the generalized condition. Members of the Draunculidae also have a thickened cuticular helmet which projects anteriorly forming the circumoral elevation and posteriorly so as to surround the anterior end of the esophagus.

**SPIRURINA.** Like the Camallanina, this suborder contains no forms with ventrolateral cephalic papillae and true lips, if present, are represented only by rudimentary apical lobes. The first superfamily Spiruroidea shows a marked tendency toward the formation of false lips, *pseudolabia*, developed from the prohabdions of the stoma while the second superfamily, Filarioidea, is characterized by the absence of both lips and *pseudolabia*. In their place there may be various types of labial structures. Within the entire suborder the internal circle of papillae is reduced, rudimentary or apparently absent.

**Spiruroidea.** The majority of spiruroids (Fig. 58) have two lateral *pseudolabia* but there is one exceptional group, the Thelaziidae. This group is apparently the most primitive of the superfamily and within it the development of *pseudolabia* is reproduced. The Thelaziinae, Spirocerinae, and Ascaropinae contain forms with a rounded to hexagonal oral opening, the hexagonal form apparently corresponding to rudimentary apical lobes of six original lips. The internal circle of papillae is slightly reduced in all forms except *Physoccephalus* in which it is rudimentary. The externodorsals and externoven-

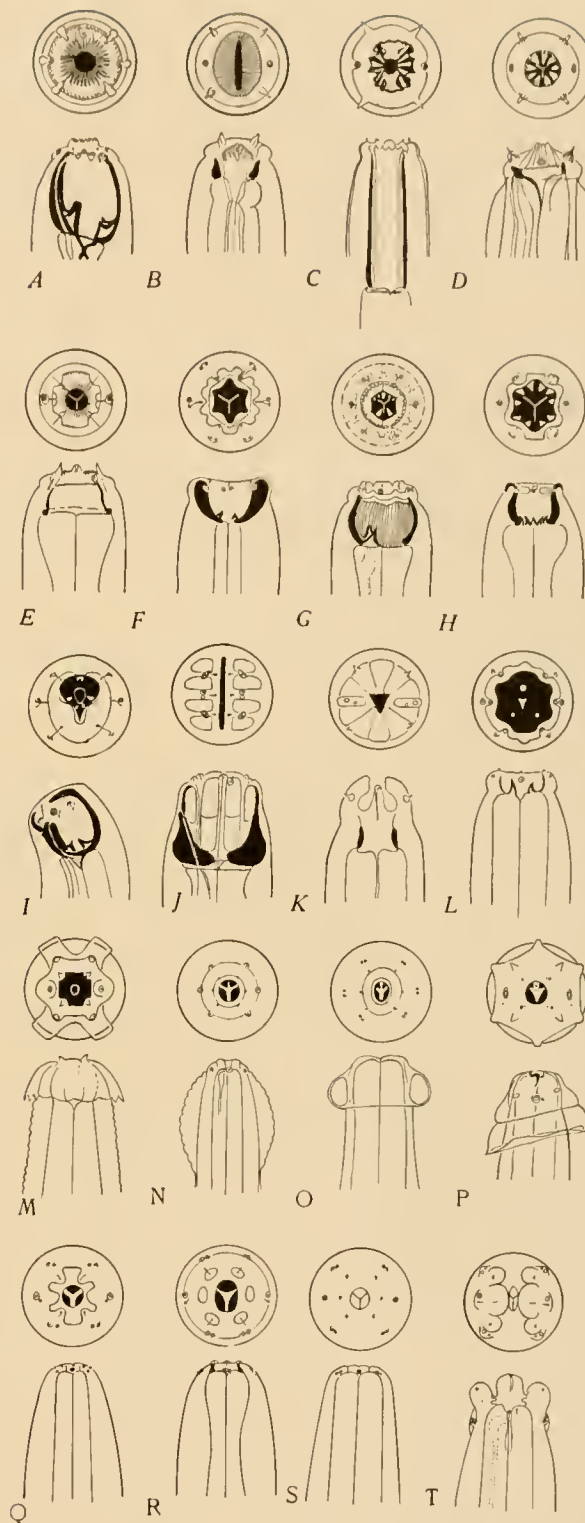


FIG. 56.

Cephalic regions in the Strongylina. A-E—Strongylidae. F-H—Syrnagidae. I—Ancylostomatidae. J—Diaphanocephalidae. K—Cloacinidae. L-P—Trichostrongylidae. Q-R—Pseudolidae. S-T—Metastrongylidae. A—*Strongylus equinus*; B—*Murshidia falcifera*; C—*Cylindropharynx rhodesiensis*; D—*Oesophagostomum dentatum*; E—*Cylicococyclus insignis*; F—*Syngamus trachea*; G—*Deletraccephalus demidatus*; H—*Stephanurus dentatus*; I—*Xecator americanus*; J—*Kaliccephalus* sp.; K—*Zoniolaimus setifera*; L—*Amidostomum cingii*; M—*Epomidiostomum uncinatum*; N—*Allintoshius nycticeius*; O—*Cheirapteronema globocephala*; P—*Trichoileiperia pearsei*; Q—*Filariopsis arator*; R—*Stenurus minor*; S—*Dictyocaulus filaria*; T—*Metastrongylus elongatus*. B—After Witenburg, 1925, Parasit. v. 17(3). C—After Yorke & Maplesstone, 1926. Nematode parasites of vertebrates. L—After Wehr, 1933, J. Wash. Acad. Sc., v. 23(18): 391-396. M—After Wetzel, 1931, Proc. U. S. Nat. Mus. (2864) v. 78(21): 1-10. Q—After Wehr, 1935, J. Wash. Acad., Sc., v. 25(9). Remainder original.

trials are distinctly separate from the laterodorsals and lateroventrals in all members of the family but they are near the size of the laterodorsals and lateroventrals in some forms, (*Thelazia californiensis*, *Pseudofilaria pertenuis*, *Ascarops strongylina*) and are reduced or rudimentary in other forms (*Cylicospirura subaequalis*, *Spirocerca lupi*). In many of the species one notes six cuticular projections of the prostom (*Spirocerca lupi*, *Ascarops strongylina*). As shown by Chitwood and Wehr (1934) the third stage larva of *Physacephalus sexalatus* has both the six rudimentary labial lobes and six internal cuticular projections of adult *Ascarops*. The circumoral membrane (labial lobes) disappear in the adult and the original internal cuticular projections assume the form of paired trilobed lips which are termed pseudolabia. It is notable that these projections bear the internal circle of papillae but the papillae are rudimentary, not merely reduced as in other thelazids. It is on the basis of these observations that the heads of other spiruroids are interpreted.

The family Spiruridae apparently contains the next most primitive representatives of the Spiruroidea. In these forms the pseudolabia are usually trilobed and with the exception of *Hedruris* they do not bear the external circle of papillae. In the Habronematinae (*Habronema*) and Hedrurinae (*Hedruris*) the median pairs of the external circle are very close together or partially fused, there being an accompanying reduction in the size of the dorsodorsals and ventroventrals while in the Tetramerinae (*Tetrameres americana*) and Spirurinae (*Protophysa* spp., *Mastophorus* spp.) there are four compound papillae due to more or less complete fusion. Labial structures are highly varied in this group and very valuable as generic and specific characters. Paired medial interlabia are present except in the Spirurinae and their shape, relative size

and complexity make very useful taxonomic characters (*Tetrameres*, *Hedruris*, *Seurocyneca*, etc). The pseudolabia are diverse in size, gross appearance and sometimes they have characteristic dentition. (*Mastophorus* vs. *Protophysa*). *Tetrameres americana* is anomalous in that the female has neither pseudolabia nor interlabia, a sexual dimorphism coinciding with the degeneration of the female to the form of a reproductive sac.

The family Aeuariidae is interpreted as being most closely related to the Spirurinae of the family Spiruridae. As in the latter subfamily, there are only four well developed papillae, these being apparently the completely fused dorsodorsal-laterodorsals and ventroventral-lateroventrals. Unlike spirurids, the pseudolabia of aeuariids are not trilobed and they bear the four papillae. Projecting posteriorly from the pseudolabia aeuariids always have some type of cuticular ornamentation these ornaments taking the form of eordons in the Aeuariinae, a spined cephalic collar in the Seuratiinae, and four variously formed appendages in the Schistorophinae.

Passing now to the Gnathostomatinae we find that the pseudolabia have assumed a more massive size, become fleshy, but retained their lobed character. There are four double papillae in all forms, the degree of fusion varying in the different genera. Of this family the Spiroxyinae is undoubtedly the most primitive for it contains such forms as *Spiroxya contorta* which superficially resemble *Protophysa* and *Mastophorus* of the Spirurinae. The subfamily Spiroxyinae differs from the Spirurinae in that the pseudolabia are massive, and bear the external circle of papillae in the former subfamily while they are inconspicuous and the papillae situated posterior to them in the latter subfamily. Gnathostomatids such as *Tanqua* have similar papillae but the pseudolabia are more irregularly

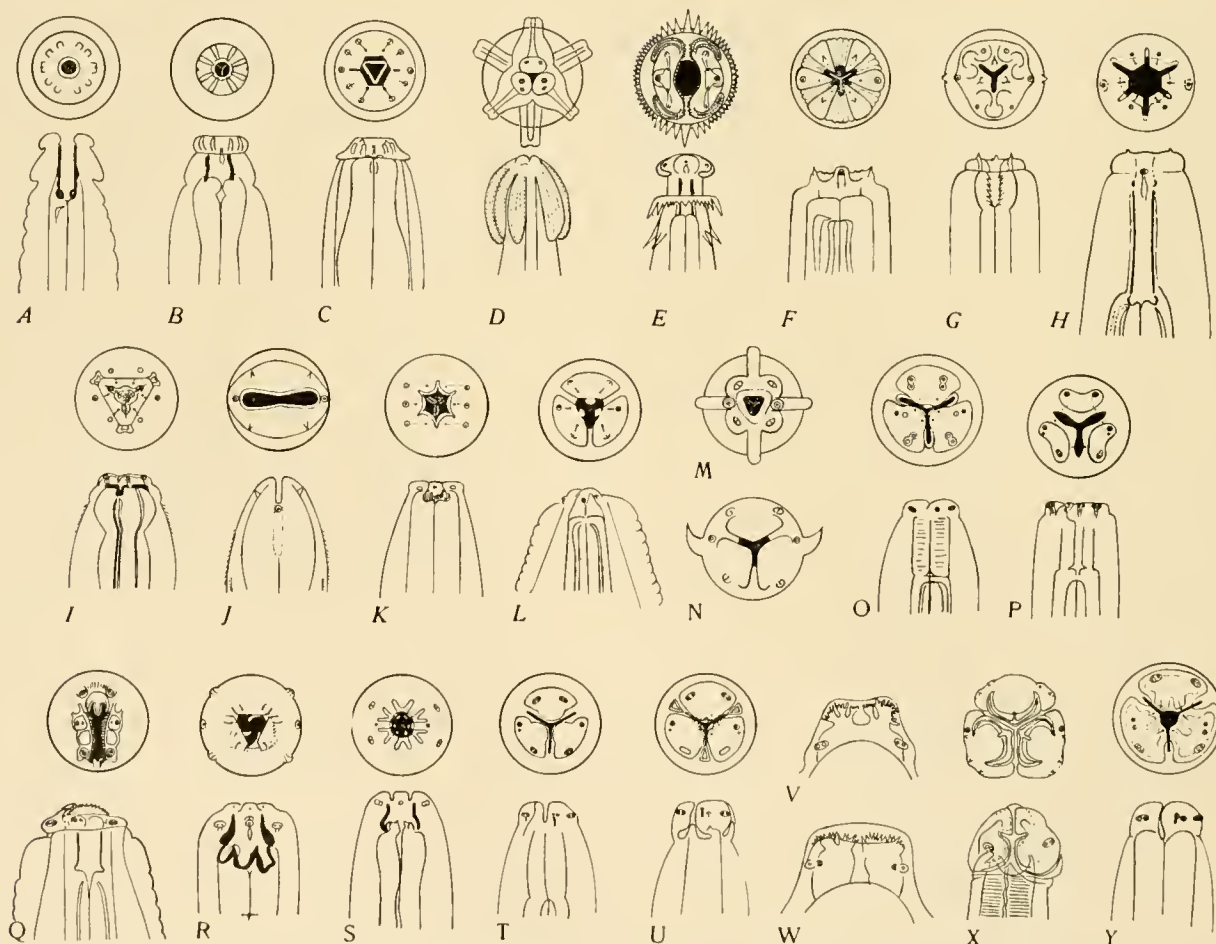


FIG. 57.

Cephalic regions in the Ascaridina. A-C—*Thelastomatidae*. D-H—*Atractidae*. I-J—*Rhigonematidae*. K-N—*Oxyuridae*. O—*Cosmocercidae*. P-Q—*Kathlanidae*. R-T—*Heterakidae*. U-Y—*Ascarididae*. A—*Leidyneema cranifera*; B—*Proterellina floridana*; C—*Aururus philippinensis*; D—*Pulchrocephalus* sp.; E—*Heth dimorphum*; F—*Atractis* sp.; G—*Crossocephalus viviparus*; H—*Probstmayria vivipara*; I—*Rhigonema infectum*; J—*Iethycephalus* sp.; K—*Oxyuris equi*; L—*Enterobius vermicularis*; M—*Aspicularis tetraptera*; N—*Dermatoxys veligera*; O—*Cosmocercoides dukae*; P—*Spiranocera affine*; Q—*Cissophylus roseus*; R—*Subu-*

*lura distans*; S—*Aulanoccephalus peramelis*; T—*Heterakis gallinae*; U—*Pocrocaecum cheni*; V—*Polydelphis quadricornis*; W—*Polydelphis boddaerti*; X—*Parascaris equorum*; Y—*Ascaris lumbricoides*. A-B—After Chitwood, 1932, Ztschr. Parasit., v. 5(1). C—After Chitwood & Chitwood, 1934, Philipp. J. Sc., v. 52(4). S—After Baylis, 1930, Ann. & Mag. Nat. Hist., s. 10, v. 5. U—After Hsu, 1933, J. Parasit., v. 19(4). V-W—After Baylis, 1921, Parasit., v. 12(4). X—After Yorke & Maplestone, 1926, Nematode parasites of vertebrates. Remainder original.



lobed and posterior to them there is a large cephalic bulb formed by the anterior expansion of four internal posteriorly extending closed sacs, the ballonets (*Tanqua*). Neither the Ancyraeanthinae nor the Spiroxyinae have a cephalic bulb but some authors have recorded ballonets in *Ancyraeanthus*. The cephalic bulb apparently functions as a holdfast, being collapsed when the anterior end is inserted into the mucosa and thereafter being inflated. Spines or retrose annulation are provided to aid in this function. *Ancyraeanthus* with four posteriorly directed cephalic appendages resembles *Schistorophus* of the Acanthiidae but the incomplete fusion of the cephalic papillae and the lobed fleshy pseudolabia seem to definitely place it in the Gnathostomatidae.

The Physalopteridae apparently represent the final conclusion of evolutionary tendencies in the Spiruroidea. Here we find paired, massive fleshy, unlobed pseudolabia bearing both amphids and four completely fused compound papillae (laterodorsal-dorsodorsal and lateroventral-ventroventral). The various species of this family have been divided into genera by Schulz (1927) on the basis of their dentition. The genus *Physaloptera* is characterized by the presence of four teeth on the internolateral face of each pseudolabium, an internal group of three, two being sublateral and one lateral, and a single externolateral tooth. *Thubunaca* is similar but the teeth on one side are always rudimentary. *Abbreviata*, has the same lateral teeth but instead of sublaterals the entire margin of each pseudolabium is dentate and there are four double submedial teeth. Whether or not these teeth correspond to the original pseudolabial lobes is problematical but their development as labial structures seem to place them clearly in the category of *odontia* which statement also applies to the teeth of *Protospirura*, *Mastophorus*, *Odontospirura*, etc. of the family Spiruridae.

**Filarioidea.** Many filarioids have neither lips, pseudolabia, nor any other types of labial structures (Fig. 59). Such forms (*Dirofilaria*, *Dipetalonema*, *Elacophora*) are placed in the family Dipetalonematidae. They are characterized by the absence of any structure which might be conceived to be of aid in feeding or penetration of tissue. The oral opening is rounded and bordered by a very delicate circumoral membrane. The majority of the remaining forms have some type of cephalic armature, such an armature sometimes taking the form of a circum-oral elevation which may bear lateral (*Dicheilonema*) or other anterior tooth like projections (pseudonechia), sometime taking the form of a sclerotized\* helmet (Squamifilaria), sometimes having both circumoral elevation and helmet (*Dicheilonema*), and sometimes taking the form of lateral sclerotized tridents (*Diplotriacna*). These forms are all included in the family Filariidae. The remaining two families, Stephanofilariidae and Desmidoecercidae each contain but one genus and may later be more closely associated with the other two families. The former family has one or two circles of cephalic spines while the latter is devoid of external armature but possesses two internal cuticular projections of the prostom which may be homologous to the pseudolabia of spirurioids. In the number of cephalic papillae the super-family Filarioidea is a remarkably constant group. There are always eight subequal large papillae which tend to take the form of two circles. However, we interpret these papillae as representing a subdivided external circle and the dorsodorsal and ventroventrals are usually anterior (*Dicheilonema*, *Dirofilaria*) to the laterodorsals and lateroventrals. The internal circle is apparently absent except in a few genera where it is represented by reduced internolaterals (*Dipetalonema*, *Litomosa*, and *Desmidoecerca*). Many writers would interpret the four anterior papillae of filarioids as the internal circle but we cannot do this because in our comparative studies it is notable that throughout the entire Phasmodia there is a tendency toward reduction in papillary size. This tendency affects the internal circle first, and thereafter the externomedians. Furthermore, the rearrangement of the external circle into two circlelets as a tendency in the order Spirurida is noticeable in *Micropleura* (Dracunculioidea) and *Pseudofilaria* (Spiruroidea) in both of which there is the full component of papillae.

## B. APHASMIDIA

Aphasmodians have externally modified amphids in all except the parasitic forms and even in these the modification persists in many of the Mermithoidea. Filipjev (1918, 1929, 1934) used the morphology of the amphids as one of the prime char-

acters of major groups. More recently Stekhoven and de Coninck (1933) have reaffirmed such usage with modification. Of the many amphidial variants, there are three primary types in the Aphasmodia, these being the *spiral*, *circular*, and *cyathiform* (pocket-like). One easily recognizes transitions from *unispire* to *dispire* and *multispire*, and other series from *unispire* through *question mark*, to *shepherds crook*; these latter may be termed modified spiral amphids. Transition between *unispire* and *circular* is also an obvious step often indicated by a persistent break in the circle. Stekhoven and de Coninck (1933) further derive the *reniform* (transversely elongate) amphids of *Chromadora* from the circular amphids of *Microaimus*. Interrelationship of these amphidial types seems scarcely questionable and this fact is used as a basis for the order Chromadorida.

The cyathiform type of amphid, characteristic of the order Euphlida, seems at first glance to be of an entirely different formation but as we shall see later, it also appears to have been derived from something close to the *unispire*.

Cephalic sensory organs in the Aphasmodia universally have one point in common, the lateral papillae of the external circle are externolateral rather than ventrolateral in position. This is correlated with the post labial position of the amphids and is, perhaps, more primitive than the rhabditoid (and general phasmodian) arrangement. The size of cephalic setae presents another interesting field for observation; the external circle is always larger than the internal circle and whether the external circle is subdivided (*Plectus*, *Laimella*) or not (*Paracanthocheilus*, *Anticoma*, *Theristus*) the elements are always of two sizes. If there are four large setae these are laterodorsal and lateroventral, but if there are six they are dorsodorsal, ventroventral and externolateral. The components of the internal circle are often papilla like and have been overlooked by many observers; the smaller members of the external circle may also be overlooked. It may be stated, however, that with scarcely an exception the full component of cephalic papillae is present. Supplementary cephalic papillae or setae also occur and are very apt to cause confusion in the nomenclature. Two or more pairs of sublateral setae next to the amphid (paramphidial setae) are of the most common occurrence such being quite common in the Axonolaimoidea and Monhysterioidea. The only case of apparently true duplication of cephalic setae occurs in some monhysterioids (*Theristus*) in which the externolaterals are double. Mergence of somatic with cephalic setae (or papillae) is an unusual but not uncommon phenomenon. In such cases (*Eustrongylides*, *Mononchus*, *Metachromadora*) the sublateral or submedial somatic setae extend to the head region and become confused with the external circle of cephalic setae. Such added setae may become so numerous as to completely obscure the normal symmetry (*Steineria*). Fusion of cephalic sensory organs, so common in the Phasmodia, seems to be non-existent in the Aphasmodia.

Labial structures are entirely too diverse in this class for one to make satisfactory general statements. Both six and three-lipped forms occur in the two orders but six lips are definitely preponderant.

**MONHYSTERINA.** In cephalic sensory organs the suborder Monhysterina (Fig. 60) exhibits no real distinguishing character from the Chromadorina, one can speak only of tendencies. The lips may be well developed, entire (*Plectus*), they may be represented only by the apical lobe (*Axonolaimus*) or they may be absent (*Sphaerolaimus*). In no instance are lips obviously replaced by cheilostomatal or prostomatal rugae.

**Plectoidea.** The Plectoidea is undoubtedly one of the most interesting groups of the entire Aphasmodia for it contains the potentialities of every structural diversity of the subclass. In tactile organs the great majority of the forms are uniform having an internal circle of six papillae and a subdivided external circle of six papillae (dd., vv. and el.) and four setae (ld. and lv.). Paramphidial setae are unknown in the group. The diversity of amphidial form in the group provides clues to the relationships of the whole Aphasmodia. In *Anonchus mirabilis* and *Plectus rhizophilus* one sees the typical *unispire* amphid, a double contour structure, each edge being the side of the groove. In *Aphanolaimus aquaticus* and *Camacolaimus prytherchi* there are nearly closed, *unispire* amphids of single contour but if one observes these en face, one sees that the central protuberance is present. These amphids are also *unispire* grooves. The broken circle (single contour) amphid of *Lepidolaimus marinus* has not been studied en face but other species of the genus are known to have *unispire* amphids. *Anaplectus granulatus* (*Plectus granulatus*) is the final summation of all others for it combines features of the circular, *unispire* and cyathiform amphids. One might even term it a "universal amphid." At the surface it is a transversely elliptical, but internally it is both *unispire* and cyathiform. One might argue

\*The term sclerotized is used in the remainder of this text to indicate hardening without signifying the chemical composition. Eventually the chemistry of specialized cuticular structures will be discussed. Though many nemic structures superficially resemble chitin, this substance has been demonstrated only in the egg shell.





FIG. 58.

that the plectoid amphid came to its formation through submergence of a spiral amphid or that the spiral amphid developed from the plectoid through emergence. In either case, this type must be considered a common denominator of the Aphasnidia.

De Coninck (1935) has recently placed the family Bastianiidae in approximate relation with plectoids on the basis of amphidial and male supplementary organ characters. In this group he places *Prismatolaimus*, *Tripyla*, *Trilabus* and *Bastiania*. Gross similarity in esophagi support his view but the writers cannot accept it. The three former genera seem best placed in the Enoplina (Tripylidae). De Coninck notes variation in *Bastiania parvifilis* from unispire to transverse (cyathiform). The writers may add that in *Bastiania exilis* a single specimen had one unispire and one broken circle amphid. *Bastiania* and *Odontolaimus* are odd plectoids in having 10 cephalic setae, the external circle being partially subdivided. The oddity goes even further in that the six anterior setae (dd., el., vv.) are slightly longer than the four posterior (ld. and lv.). Thus we find the 6-6-4 symmetry of Plectoids remains but the size relationships in the two external subdivisions are reversed. The genera *Bastiania* and *Odontolaimus* seem best placed in the family Bastianiidae as an appendix to the Plectoidea.

*Axonolaimoidea*. In this superfamily one finds the same base symmetry as in the Plectoidea, namely an internal circle of six papillae, a subdivided external circle of six papillae or short setae (dd., el. vv.) and four long setae (ld. and lv.). In addition paramphidial setae are apt to be found just posterior to the cephalic setae. Such setae may be four (two pairs) in number, preamphidial (*Sabatieria longicaudata*) or postamphidial (*Laimella quadrisetosa*) or they may be eight in number (four pairs) (*Odontophora angustilaima*, *Axonolaimus subsimilis*, *A. odontophoroides*).

The family Comesomatidae is rather uniform in having multispire amphids but the Axonolaimidae, are even more diverse than the Plectidae. *Araolaimus* (*Araolaimoides*) *zosterac* *Axonolaimus subsimilis* and *Odontophora* have rather distinct double contour unispire amphids, *Araolaimus cylindrolaimus* has a broken circle to single contour amphid and *Cylindrolaimus communis* a circular amphid. The amphids show numerous gradations in elongation from the unispire type in *Axonolaimus subsimilis* to the inverted U of *Axonolaimus spinosus* and shepherd crook, *Pseudolella granulifera*. As in the Plectoidea, each external amphid is a spiral groove, posterior closure of which leaves a central elevation. *Aegialolaimus elegans* represents the sole instance of multispire amphids in the Axonolaimidae. However, the Diplopeltinae introduce still another variant, the presence of lateral shields accompanying the amphids (*Didelta*). In this group one may trace a repetition of the unispire—question mark—circular amphid development.

*Monhysteroida*. Monhysteroids have great diversity in cephalic symmetry. The most common arrangement is an internal circle of six papillae and an undivided external circle of 10 or 12 setae. Stekhoven and de Coninck (1933) characterized the group as typically hexaradiate. The one unifying characteristic is that the amphids are nearly invariably circular.

The family Linhomoeidae includes some forms such as *Metalinhomoeus typicus* and *Desmolaimus zelandicus* with a subdivided external circle of six papillae and four setae (ld. and lv.) or 6-6-4 symmetry; others such as *Paralinhomoeus lepturus*, *Monhysterium transitans* and *Halinema spinosum* with an undivided external circle of six short and four long setae or 6-(6-4) symmetry; and still others such as *Linhomoeus elongatus* with an undivided external circle of four short and six long setae or 6-(4-6) symmetry. There usually are, in addition, eight paramphidial setae. The genus *Sphaeralaimus* presents an array of setae that has not as yet been satisfac-

torily interpreted. One finds the normal internal circle of six papillae followed by a circle of six short setae (? dd., el. and vv.) followed by a circle of 16 setae, in eight pairs, two pairs sublateral, two submedial; in addition there are two pairs of preamphidial setae and somatic setae arranged in eight longitudinal rows (submedial and sublateral). One might, provisionally, assume that four papillae of the external circle (ld. and lv.) have been overlooked and somatic setae have added to cephalic setae. On this basis the symmetry may be characterized as 6-10 (4-6) + 16 (8-8) + 4 (2-2).

Members of the Monhysteridae sometimes have but six elongate setae (6-4-6) such as *Cyrtolaimum obtusicaudatum* but more commonly there are 10 or 12 setae in the external circle, *Halanonchus macramphidum* and *Theristus setosus* represent the more typical arrangement with six papillae in the internal circle, six short and six long setae in the external circle. Of the latter circle the longest six are the dorsodorsal, ventroventral and dorsolateral. Duplication of the external lateral results in a large dorsolateral and a small ventrolateral. Such symmetry may be characterized as 6-12 (6-6). Paired sublateral pre-amphidial setae are also present. *Scaptella cincta* has a peculiar combination of axonolaimoid and monhysterid symmetry. The presence of 6 short setae in the internal circle and 12 setae in the external circle is characteristically monhysterid but the external circle consists of setae in three sizes; four are very long (ld. and lv.), 6 are moderately long (dd., vv., and dl.) and two are short (vl.). Therefore, the external circle might be characterized (2-6-4). *Omicronema litarium* and *Steineria* sp. represent types with increased cephalic setae. In the former instance three circles are described, an internal circle of six setae, an intermediate circle of four sublateral setae and an external circle of 18 setae in six groups of three, an arrangement which may be noted 6-4-18. It seems possible that a restudy of *Omicronema* will show it to be a sphaerolaim. *Steineria*, on the other hand, is typically monhysterid in character having an internal circle of six papillae and an external circle of 10 or 12 setae (according to the species). In addition to the cephalic setae, numerous somatic setae are grouped anteriorly in eight longitudinal rows, four submedial and four sublateral.

*Siphonolaimus* has an internal circle of six papillae, an external circle of 10 setae of which the four sublaterals (ld. and lv.) are the largest; this 6-10 (6 + 4) symmetry is more like *Paralinhomoeus* than any other forms discussed.

The circular amphid with central fleck is often mentioned as a characteristic of linhomoeids but the central fleck is neither confined to that group nor obvious in all members. As in plectoids, a central elevation represents the inner side of the amphidial groove, be it circular or spiral. The relative height between grooves determines the gross "presence" or "absence" of a central fleck.

Paramphidial setae of some type are nearly always present in monhysteroids; most commonly these are four in number, sublateral preamphidial in position. In addition to which there may be four sublateral postamphidial or four submedial preamphidial setae.

Six separate or three more or less lobed lips may be present in monhysteroids but if so, they are generally reduced, the labial elevation bearing faint longitudinal ridges; which are developments of the cheilorhabdions.

*CHROMADORINA*. Members of this suborder show all of the diverse symmetry arrangements (Fig. 61) of cephalic setae and nearly all of the amphidial forms present in monhysterids. True lips are seldom apparent but very highly developed cheilostomatal rings usually take their place.

*Chromadoroidea*. The family Mierolaimidae is characterized by unispire, postlabial amphids, an internal circle of six papillae and a subdivided external circle of six papillae or short setae and four long setae, 6-6-4 symmetry. True lips are

FIG. 58.

Cephalic regions in the Camallanoidea, Draecunuloidea and Spiruroidea. A-C—Camallanidae. D-F—Cucullanidae. G-H—Philometridae. I-J—Draecunculidae. K-V—Thelaziidae. W-KK (except Z)—Spiruridae. LL-NN & Z—Acanthidae. OO-PP & UU-VV—Physalopteridae. QQ-TT—Gnathostomatidae. A—*Procammallanus fulvidraconis*; B—*Camallanus sweeti*; C—*Camallanus microcephalus*; D—*Omicia hoepfli*; E—*Haplonema sinensis*; F—*Cucullanus truttiae*; G—*Micropleura vivipara*; H—*Philometra rubra*; I—*Draecunculus medinensis*, male; J—*Draecunculus medinensis*, female; K—*Thelazia californiensis*; L—*Pseudofilaria pertusae*; M—*Oxyuris nana*; N—*Spiracera lupi*; O—*Cyliocephalus subaequalis*; P—*Acaecops strongylina*; Q—*Physicocephalus sexualatus*; R—*Simondia paradoxa*; S—*Leuris leptoccephalus*; T—*Streptopharagus armatus*; U—*Rictularia coloradensis*; V—*Gongylophorus pulchellus*; W—*Spirura rhypleurites*; X—*Protospirura numidica*; Y—*Rhabdochona kidderi*; Z—*Stegophorus stellae-polaris*. AA—*Spinitectus carolini*; BB—*Habronema microstoma*; CC—

*Draschia megastoma*; DD—*Seurocyanea uncinipenis*; EE—*Parabronema indicum*; FF—*Odontospirura cettiopsis*; GG—*Mastophorus muris*; HH—*Cystidicola stigmatura*; II—*Hedurus* sp.; JJ—*Tetraneura americana* (male); KK—*Ascarophis harwoodi*; LL—*Acaecia anthuris*; MM—*Yseria coronula*; NN—*Schistophorus cucullatus*; OO—*Skrjabinoptera phrynosoma*; PP—*Thulineta leiodiplosmae*; QQ—*Spiroxya canturia*; RR—*Hartertia galinarum*; SS—*Tanqua tiara*; TT—*Ancyraacanthus pinnatifidus*; UU—*Abbreviata mordens*; VV—*Physaloptera maxillaris*. A—After Li, 1935, J. Parasit., v. 21(2). B—After Moorthy, 1937, J. Parasit., v. 23(3). D-E—After Hsu, 1933, Parasit., v. 24(4). L—After Sandground, 1935, Rev. Zool. Bot. Afr., v. 27(2). EE—After Baylis, 1921, Parasit., v. 13(1). FF—After Wehr, 1933, Proc. U. S. Nat. Mus., (2958) v. 87(17). Z—MM, NN—After Wehr, 1934 J. Wash. Acad. Sc., v. 24(8). Remaining figures based upon Chitwood & Wehr, 1934, Ztschr. Parasit., v. 7(3) and unpublished observations.



rudimentary or absent, and 12 more or less projectable cheilo-stom rugae are present. Chromadorids differ from microlaimids only in that the amphids are moved anteriorly, usually to the level of the cephalic setae, and vary from unispire (*Odon-tonema*) to reniform (*Prochromadora*). The Cyatholaimidae, and Tripyloididae, differ from microlaimids and chromadorids in having an undivided external circle. In all forms studied by the writers there are four small and six large (dd., el., and vv.) papillae or setae in the external circle. De Coninck (1935) characterizes cyatholaimids as having two circles of six papillae and an external circle of ten setae. Since he specifies no form as exemplifying this condition we must judge by our own observations. In some cyatholaimids particularly members of the Choanolaiminae such as *Halichoanolaimus robustus*, the fiber trunk of each of the papillae of the internal circle shows in optical cross section much like a papilla but then it bends nearly at right angles over the stomatal cavity before reaching the true sensory terminus. Thus, by optical illusion one may see more papillae than exist. Rudimentary lips and heavy stomatal rugosities (usually 12) are conspicuous features of most members of the Cyatholaimidae (*Gammonema*, *Halichoanolaimus*, *Paracanthouchus* and *Pomponema*) while three well developed lips occur in members of the Tripyloididae. Both circular and unispire amphids are known in these families but multispire are the rule.

**Desmodoroidae.** Like microlaimids and chromadorids members of this superfamily have an internal circle of six papillae and a subdivided external circle of six papillae or short setae and four long setae (laterodorsal and lateroventral). *Monoposthia heralata* and *Spirina parasitifera* are typical examples. Somatic setae are quite apt to become nearly cephalic in position as in *Metachromadora onyxoides* and *Croconema mamillatum* but by careful study one can usually segregate the two types. Helmet formation is often a conspicuous desmodoroid feature but this has been previously mentioned with the cuticle. Amphids in desmodoroids are primarily spiral, the unispire prevailing (*Epsilonema*, *Spirina*) but closed unispire (*Metachromadora onyxoides*), circular (*Monoposthia heralata*), multispire (*Richtersia beauforti*) and elongate or shepherd's crook amphids (*Ceramonea*) also occur. True lips are rudimentary, sometimes indicated by six rudiments and stomatal rugae often replace them but these also disappear with reduction in stoma.

**Desmoscolecoidae.** The amphids of desmoscolecoids are a characteristic feature, usually being described as vesiculate. They are rather bubble like but internally one may distinguish evidences of a unispire character. Due to their small size the head of only one species, *Desmoscolex americanus*, has been studied en face. In this form there are six minute lips each bearing at least one (?two) papillae. Four large cephalic setae are known in all forms. Thus we may presume a possible desmodoroid relationship.

**ENOPLINA.** Members of the suborder Enoplina may have three, six or no lips, cephalic papillae or cephalic setae, but they are all similar in having cyathiform amphids.

**Tripyloidea.** Included in this group (Fig. 62) are many forms which show relationships to other groups. The Mononchidae, with six lips, an internal circle of six papillae and an external circle of ten papillae, seem clearly related to dorylaimoids. The family Tripylidae includes closely related forms with diverse symmetry. The genus *Tripyla* is characterized by three lips, an internal circle of six papillae and a subdivided external circle of six papillae or short setae and four papillae or long setae (ld. and lv.). *Trilobus longus* and *Prismatolaimus intermedius* have six small lips (apical lobes), an internal circle of six papillae and an external circle of 10 setae, four being short and six long (ld., el., and vv.). De Coninck places these forms in the Bastianiidae close to *Plectus* but we cannot agree with this placement on the basis of esophageal characters. Undoubtedly the Tripyloidea is the most primitive group of the order Enoplida, and hence most closely related to the Plectoidea but it is customary to place primitive groups with the forms that they gave rise to rather than with other primitive groups.

The family Ironidae includes forms which may (*Ironus*, *Ironella*) or may not (*Cryptonchus*) have cephalic setae. If such are present the external circle is subdivided with six anterior papillae or setae and four posterior setae (ld. and lv.). Lips may be moderately distinct but are usually rudimentary or absent.

**Enoploidea.** With the exception of the Oxystomininae the Enoploidea (Fig. 63) hold quite closely to a six-ten symmetry with an undivided external circle of which there are four small and six large setae (dd., el., and vv.). In the single exceptional group, the external circle is subdivided, with six large

anterior and four large posterior setae (*Halalaimus carolinensis* and *Oxystomina alpha*). Lips are seldom well developed in enoploids but one finds three massive apical lobes in *Enoploides* and *Enopholaimus*, three small apical lobes in *Enoplus*, *Anticoma* and *Anaplostoma*. Six small apical lobes are general in the Oncholaiminae but even such lobes are not apparent in forms such as *Balbella tenuidens* and *Encheidium pauli*.

In most enoploids the amphids are typically cyathiform but in the Oxystomininae they are longitudinally elongate (*Oxystomina alpha*, *Halalaimus carolinensis*). De Coninck (1936) considers the oxystomins related to the genus *Araolaimus* and derives the amphids by elongation. This point requires more critical study. If the oxystomin amphid is a modified spiral, then it must be an open groove while if it is an elongate pocket, it is open only at its anterior end. Thus far such information has not been presented.

**DORYLAIMINA.** Like the Enoplina, the suborder Dorylaimina (Fig. 64) is characterized by cyathiform amphids but in parasitic members of this group the amphids may become externally pore-like. The cephalic papillae of dorylaimins, like those of mononchids and phasmodians, never take the form of setae.

**Dorylaimoidea.** Members of this group for the most part, have six rather well developed lips; sometimes the lips are set off from the remainder of the body as in mononchs and rhabditids. The full component of cephalic papillae are recognizable, there being an internal circle of six and an external circle of 10. Members of the latter circle are usually of two slightly different sizes and at two different levels on the lips. The large cyathiform amphids are situated just posterior to the labial region. Thorne (1935) described the amphids of diptherophorids as crescentic with reminiscences of spiral features.

**Mermithoidea.** Functional lips do not occur in mermithoids, the original lips being represented only by fiber tracts of the six papillary groups. These fiber tracts are (*Mesomermis bursata*, *Hexameris albicans*) usually referred to as "papillae" in the literature. Careful study shows each of the four submedian "papillae" end in three tactile sensory organs (true papillae) while each of the laterals end in two; this corresponds exactly to the normal papillary symmetry with 16 papillae. The amphids may be associated with the lateral lip rudiment (*Hexameris albicans*) or they may be quite separate from it (*Mesomeris bursata*). One finds all manner of amphidial types from large cyathiform as in *Mesomeris* to externally minute pore-like structures as in some *Hexameris*. In addition, instances are known in which the amphids are joined dorsally by a fiber tract, a condition particularly common in the genus *Paramermis*. A shift of the oral opening ventrally is not uncommon in mermithoids (*Eumermis*, *Limnomermis*) and this migration is not accompanied by a shift of cephalic papillae, though the amphids may assume a more dorsal position.

**Trichuroidea.** Cephalic papillae and amphids have been studied in only one member of this superfamily, *Trichuris suis*. In this instance lips are absent, six papillae and externally pore like amphids were observed. The position of the lateral papillae (presumably of the external circle) in a true lateral position seems distinctly to indicate aphasmodian relationships.

**DIOCTOPHYMATINA.** Dioctophymatoids are well known for their cephalic symmetry or lack of it. Lips are absent in all members of the group. The oral opening in the Dioctophymatidae is surrounded by a cuticular circumoral membrane while in the Soboliphymatidae the body extends anterior beyond the true oral opening forming an oral sucker. Presence of modified somatic muscle tissue and body cavity in this sucker is distinct evidence that the true oral opening should be regarded as the base of the sucker cavity; presumably, the cephalic papillae are on its internal surface.

"Cephalic papillae" are so numerous in members of the Dioctophymatidae (*Eustrongylides ignotus*, *Dioctophyma renale*) as to completely confuse one first observing them. The total number and arrangement varies within the species but certain papillae remain constant (Fig. 64). These latter are the true cephalic papillae; the others are considered as somatic papillae extending anteriorly from the lateral areas. There is an internal circle of six papillae and an external circle of four small (ld. and lv.) and six large papillae (dd., el. and vv.). This symmetry is the same as that to be found in a large part of the Dorylaimoidea and Enoploidea. It is in definite opposition to that found in phasmodians such as the Spiruroidea to which these nemas are sometimes compared. The amphids of dioctophymatids are posterior to the external lateral papillae, sometimes appearing to be narrow, cyathiform, sometimes pore-like.



## 2. STOMA

The structure of the stoma has generally been used as a taxonomic character since the beginning of nematology. Its wide use for the classification of groups of all ranks makes a thorough consideration of its evolution necessary. That its morphology has great value can scarcely be doubted by any worker in the field but the weight that may be given to its gross form seems dubious. Since the method of feeding and character of the food itself is limited by the stoma and its armature, this organ is probably more directly influenced by environment than any other. A radical change of feeding habits of closely related forms would require change in stomatal morphology if forms are to survive. Likewise it is not at all inconceivable that quite unrelated nemas coming to feed in the same manner might eventually become grossly similar as regards stomatal morphology. For the above reasons one must consider stomatal morphology very closely.

Only one author, Cobb (1919), has attempted to use stomatal morphology as a major character. This author made the "presence" or "absence" of a stoma ("pharynx," buccal capsule etc.) the basis of dividing the "Nemates" into two classes, Laimia and Alaimia. This classification based upon a single character totally without correlation with any other organ has nothing in common with other classifications. Though their viewpoints may be diametrically opposed, the classifications of other writers all have considerable in common and they all are at complete variance with that of Cobb. The "presence" or "absence" of a stoma seems to be a rather bad point for classification purposes since all nematodes have something corresponding to the stomatal region.

Filipjev (1934) considered enoploids such as *Leptosomatum* which have no definite clear cut stoma as the more primitive while the writers regard forms such as *Rhabditis* and *Plectus* with distinct elongated stomata as primitive. Steiner (1933) proposed a nomenclature for the parts of the stoma which we shall follow as far as possible indicating homologous regions and structures and the apparent evolutionary trends and variations as we interpret them.

The cylindrical stoma of *Rhabditis* may be divided into three primary divisions (1) *cheilostom*—lip cavity, (2) *protostom*—cylindrical part of stoma and (3) *telostom*—end cavity, which in this form is often termed the glottoid apparatus. The corresponding walls of the stoma are termed cheilorhabdions, protorhabdions and telorhabdions, respectively. The walls of the protostom, i. e., protorhabdions, in *Rhabditis* are less distinctly subdivisible into three parts (a) prorhabdions, (b) mesorhabdions, (c) metarhabdions the corresponding regions being termed prostom, mesostom and metastom, respectively. In rhabditids the division between mesorhabdions and metarhabdions is scarcely visible in many species but manifests itself more prominently in related forms. The first subdivision, i. e., prorhabdions vs. meso-metarhabdions is quite obvious and has long been recognized as the "mouth collar or mouth cuff." The basic parts of the stoma are apparently innate in the manner of their deposition and may best be observed in molting specimens or in specimens treated with reagents such as weak acids and alkalis. On the basis of studies made in this manner it would seem that the appearance of jointed protorhabdions in representatives of diverse groups is not convergence in the strict sense but rather manifestation of an innate characteristic which is ordinarily masked.

The stoma may take diverse shapes due to modifications of its parts and many different types of armature are developed according to the particular group involved. One of the most common types of armaments are teeth. Historically the term *onchia* has been most commonly applied to such structures though by derivation (*ὄνχος* = hook, the barb of an arrow) its use does not seem apt. More recently the term *odontia* (*ὀδούς* = a tooth) has been applied and seems the more proper but in such case it should not be confused with the limited definition given by Cobb (1919). This author defined *odontia* as teeth arising by modification of the labial region while the term *onchia* was used by him to denote teeth arising more posteriad. Because of the common co-existence of both *onchia* and *odontia*, (in the Cobbian sense) one has need for two terms and the writers feel that though the first term is inapt, it is nevertheless worthy of preservation. We therefore retain Cobb's definitions.

Numerous other words are commonly used in a descriptive manner in specialized groups. Thus a region of the stoma or the margin of lips may be described as *dentate* (having teeth) or *denticulate* (having small teeth); basal *onchia* in the Strongyloidea are described as *lancets*; and the term *fossor* is

used for outwardly acting teeth at the anterior extremity (often *odontia*). In some instances, as in the tylenchids, the stoma is transformed into a protrusible spear, termed a *stomatostyl*, while in others (dorylaimids) the stoma is to a greater or lesser extent filled by a large tooth, in which case the spear or stylet is termed an *onchiostyl*. Other specializations will be discussed with the various groups.

Convergence of stomatal formation accounts for the origin of stylets in four separate groups: the Tylenchoidea, of the Phasmidia, the Siphonokimidae (Monhysteroidea), some representatives (*Anguinoides*) of the Camacolaimidae (Plectoidea) and the entire Dorylaimina. Similar convergence accounts for paired jaws formed essentially by the stomata rather than the lips in the Kalicephalidae (Strongyloidea), Icthyocephalidae (Oxyuroidea) and Camallanidae and Cucullanidae (Camallanoida). One must be very hesitant in concluding relationships based upon such characters.

In describing the stoma it is the common practice to speak of certain parts or regions as being chitinized. As will be seen later, there is no real evidence that either the stoma or the denticular structures are actually chitin and we shall use the noncommittal term *sclerotized* for hardened refractive regions.

### A. PHASMIDIA

In each of the large groups of the Phasmidia some forms exist that possess a cylindrical stoma very similar to that of *Rhabditis*.

**RHABDITINA.** This suborder (Fig. 54) is divided chiefly on the base of the stoma into two superfamilies, the Rhabditoidea in which the stoma is not transformed into a stylet and the Tylenchoidea in which such a transformation has taken place.

In the Rhabditoidea there are two families, Rhabditidae and Rhabdiasidae, in which the stoma is of a generalized structure consisting of cheilostom, protostom and telostom, the protostom being cylindrical, not surrounded by strong esophageal tissue. The parts are all well sclerotized and divisions of the protostom are not distinct. It is interesting that in the parasitic genera rhabdiasids have a relatively short (*Rhabdias*) or subglobular (*Entomelas*) stoma with well sclerotized walls showing no indications of cheilostom or telostom. This transformation takes place in the development of the individual after it enters the host.

The family Cyndrogasteridae (*Longibucca*, *Cyndrogaster*) is probably the next most closely related group and herein we again find a cylindrical stoma, distinct cheilorhabdions and telorhabdions (in form of small plates) and a greatly elongated protostom subdivisible only into pro- and meso-metastoms. Cephalobids, differ considerably in stomatal appearance, there being a more or less cylindrical stoma in *Panagrolaimus* and a collapsed stoma in *Aerobeloidea* and *Cephalobus*. In all cases the stomatorhabdions are rather separate, giving the impression of a segmented stoma due to areas lacking in sclerotization; the extent of "degeneration" in stomatorhabdions is apparently correlated with the amount of esophageal musculature surrounding the stoma. With complete collapse of the stoma (*Daubaylia*) there is an entire absence of sclerotization and the base of the original stomatal region (telostom) is indicated only by a break in the esophageal musculature. The consequent "stomatal region of the esophagus" is termed a *vestibule*. Such a vestibule is all that remains in the related family Steinernematidae (*Neoplectana*).

The Diplogasteridae is a highly variable group containing forms which link it with the Rhabditidae, Cephalobidae, Strongyloidea and Tylenchoidea. Several series of genera are known in the Diplogasterinae. *Rhabditoides* has a cylindrical protostom sclerotized as in *Rhabditis* but the cheilorhabdions are non-sclerotized and the telorhabdions asymmetrically developed; the closely related genus *Aerostichus* has distinct cheilorhabdions but the prostom and mesostom each form a distinct cavity, followed by a modified metastom containing a large dorsal tooth. *Odontopharynx* and *Butlerius* may be considered further members of this "double stoma" series. *Neodiplogaster* may be considered as a side branch of such a series originating from a form not unlike *Rhabditoides* in which collapse of the stoma was followed by loss of sclerotization of stomatorhabdions with consequent convergence with cephalobids and steinernematids in the resulting vestibule. A second line of evolution seems to be indicated by a series from *Rhabditoides* to *Mononchoides americanus*, *Diplogaster feticar*, *Pristionchus acrivora* and terminate with *Lycolaimus*. In this series there is collapse and non-sclerotization of the metarhabdions accompanied by shortening and thickening of the pro- and mesorhabdions, the development of a massive dorsal and a

right subventral tooth and finally by complete amalgamation of these structures in *Lycolaimus*. The third and last line of evolution seems to antedate *Rhabditoides* in that the cheilorhabdions are preserved. *Tylopharynx* and *Tylenchodon* have a stoma that clearly simulates a stomastostyl, the stylet guide being formed by the cheilorhabdions, the anterior part of the stylet by prorhabdions, the shaft (or stylet) by meso-metarhabdions and basal knobs by telorhabdions. Such forms are retained in the Diplogasteridae since there is no proof that the "stylets" are protrusible. *Tylopharynx* and *Tylenchodon* form a definite link with the Tylenchidae. We have omitted remarking thus far on the presence of sclerotized rugae in the Diplogasterinae. As has been previously noted, members of this group have either no lips or much reduced lips. In many forms the prostom is longitudinally broken into numerous heavily sclerotized rugae, these rugae having much the same appearance as the internal leaf crown of strongylids. The degree of development of the rugae seems to be correlated with the size and degree of development of the dorsal tooth (*Pristionchus uerivora*, *Diplogaster fector*, *Mononchooides americanus*). As to the origin and end of the series previously mentioned, there are some who would see the series in reverse, i. e., proceeding from short stoma, amalgamated forms such as *Lycolaimus* to cylindrical stoma forms such as *Rhabditoides*. In reply we may state that study of young larvae show the series to be correctly oriented. Forms with a short or divided stoma in the adult stage have a more cylindrical, elongated, less divided stoma in the larval stage.

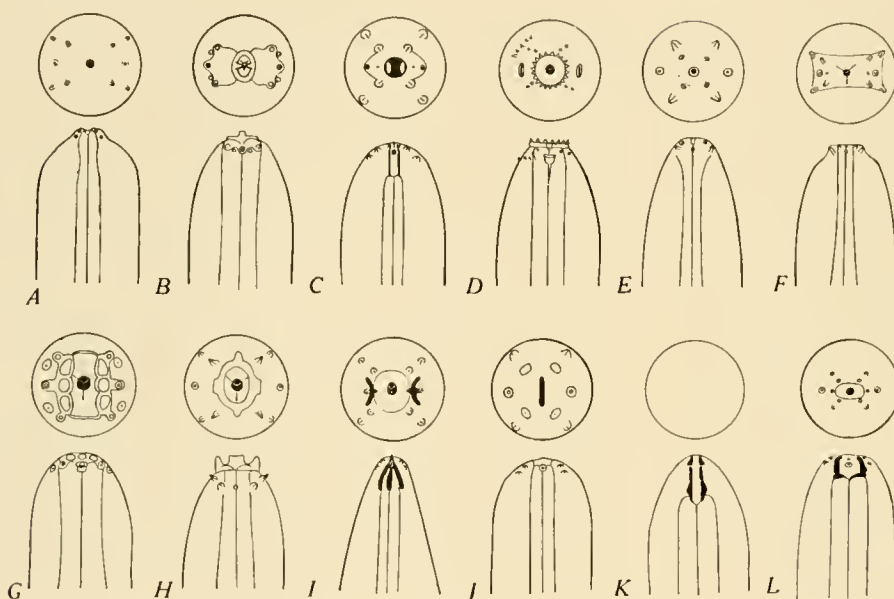


FIG. 59.

Cephalic regions in the Filarioidea. A, E-F, J-L—Dipetalonematidae. B, G-I—Filariidae. C—Desmidoceridae. D—Stephanoflariidae. A—*Diroflaria immitis*; B—*Dicheilonema rheae*; C—*Desmidocerca numidica*; D—*Stephanoflaria stilesi*; E—*Elaeophora schneideri*; F—*Dipetalonema gracile*; G—*Squamiflaria thoracis*; H—*Setaria equina*; I—*Diplotrichaena* sp.; J—*Cardianema cistudinis*; K—*Litomosoides hamletti*; L—*Litomosa americana*. E—After Wehr & Dikmans, 1935, Zool. Anz. v. 110 (7-8). G—After Toboagui, 1934, Philipp. J. Sc., v. 55 (2). L—After McIntosh & McIntosh, 1935, Proc. Helm. Soc. Wash. v. 2 (1).

Returning to the other subfamily of the Diplogasteridae, the Alloionematinae we find less variation in stomatal development. In *Alloionema* and *Rhabditophanes* the cheilostom and prostom form the functional stoma and their rhabdions are well sclerotized but not always distinctly recognizable; the meso-metarhabdions may or may not be well sclerotized but they are always surrounded by esophageal tissue and the telorhabdions are rudimentary. *Strongyloides ransomi* (Strongyloididae) passes through this stage in its larval development preceding complete collapse of the mesostom with vestibule formation. *Scelencella* of the Alloionematinae apparently proceeds even further in this line of evolution with shortening and amalgamation of the cheilostom-prostom, the result being a nearly complete convergence with *Lycolaimus*.\*

The remaining two families of the Rhabditoidea are insufficiently known for a general characterization of their stomata; we cite the figures of *Angiostoma plethodontis* (Angiostomatidae), *Diclis nira* and *Ungella seta* (Drilonematidae) as representatives of the groups.

\*The Rhabditinae—Alloionematinae—Diplogasterinae complex seems to exhaust practically all of the possible combinations of stomatal, esophageal and bursal characters. Aside from tooth formation—absence of valved bulb and cephalic characters there is little or no correlation. One might easily prefer to arrange the narrow bursate cylindrical stoma, forms of the Rhabditidae (*Rhabditoides*, *Rhabditella*) and Diplogasterinae (*Rhabditoides*, *Neodiplogaster*) together and the short stoma *Lycolaimus* with *Scelencella* in the Alloionematinae. However, on the basis of present evidence this would cause an unwarranted confusion and would be even more arbitrary than the present division.

It has been previously noted that the Tylenchoidea (Fig. 55) have a stomastostyl homologous with the stoma of rhabditoids, probably having developed through some such forms as *Tylenchodon* or *Tylopharynx*. Such a stylet consists of four basic sclerotized parts (1) cheilorhabdions (stylet guide), (2) prorhabdions (conoid or insertible part of stylet), (3) meso-metarhabdions (stylet shaft) and (4) telorhabdions (stylet knobs). The stylet guide or cheilorhabdions are best developed in tylenchids with a sclerotized cephalic region such as *Hoplolaimus* and *Pratylenchus* but may be relatively distinct in less heavily sclerotized forms such as *Neotylenchus*. The basal knobs (telorhabdions) are primarily three in number but may be bilobed, particularly in cases where they are anteriorly bent such as *Hoplolaimus bradys*\*. In tylenchids the greatest diversity is in degree of development of the basal knobs and relative size of the stylet. A few forms such as *Aphelenchus avenae*, have no basal knobs and a very delicate stylet. Others such as *Aphelenchoides parietinus* have weak knobs and a delicate stylet while *Ditylenchus dipsaci* has both moderately developed. *Hoplolaimus bradys* represents a type with massive stylet while *Paratylenchus* and *Criconeuma* have a massive and greatly elongated stylet which may extend posteriorly into the metacarpus. A few instances are known in which there is sexual dimorphism in the degree of stylet development.

The entire family Allantonematidae is characterized by stylet degeneration, the cheilorhabdions and telorhabdions being most effected by this tendency. Stylet development in this family seems to be primarily dependent upon the life history, the stylet

being best developed in very young larvae and degenerating or entirely disappearing after whatever stage has passed in which the organism enters its host animal. Thus Cobb (1928) showed that the stylet is vestigial in adult males while it is well developed in non-gravid females; the males and females copulate while free-living after which the male dies but the female re-enters its host. The stylet of the female also becomes degenerate after entrance into the host.

**STRONGYLINA.** Stomata in the suborder Strongylina (Fig. 56) give one of the clearest cases exemplifying the biogenetic law that ontogeny recapitulates phylogeny. Though the structure in the adult stage is highly varied in the first stage larva it is always of a more or less rhabditoid form. In adult strongyloids the stomatorhabdions are always heavily sclerotized, the stoma well developed and capacious while in adult trichostrongyloids and metastrongyloids the stomatorhabdions are usually weakly sclerotized and the stoma reduced or rudimentary. Though the stoma becomes reduced or rudimentary in many representatives of the Strongylina, such reduction occurs through shortening rather than through overgrowth of esophageal tissue. Vestibule formation which oc-

\*The anterior part of the stylet, as well as the cheilorhabdions are cast off with the exuvium at the last molt of *Ditylenchus*. It likewise differs in chemical nature. However, the extent of molting is no evidence of homology for the entire stomatal and esophageal lining is cast off at the last molt of *Caenillanx*, *Ancylostoma* and *Agamermis* while apparently only the cheilorhabdions molt in *Rhabditis* and first *Ancylostoma* larvae.



occurs in so many other groups (Rhabditoidea, Ascaridoidea, Spiruroidea and Camallanoidea) is conspicuously absent in the Strongyloidea.

**Strongyloidea.** First stage strongyloids have a stoma identical with that of *Rhabditis*. This stoma gradually collapses in the second stage and in the third stage it may simulate a stomatostyl. Cobb (1923) described the third stage larva of *Necator americanus* as possessing a stylet but as shown by Stekhoven (1926) this was a false interpretation. The lumen of the stoma is merely partly closed and non-functional in this stage, the so called stylet not being protrusible. A similar appearance occurs in third stage *Rhabditis* larvae when they enter the resistant phase.

In the adult stage there are two genera of the Strongylidae with a rhabditoid stoma namely *Cylindropharynx* and *Pharyngostromylus*. Interpreting on the basis of these two forms, the chief part of the stomatal wall, the so-called buccal capsule of strongyloids corresponds to the amalgamated protorhabdions of *Rhabditis*. The telorhabdions in some instances (*Cylindropharynx*, *Cylicocyclus*) may be represented by a transverse sclerotized basal plate but usually are not distinguishable. It has previously been noted that the external corona radiata seems to be homologous to the apical lobes of the original lips. The internal corona radiata appears to be a development of the cheilorhabdions (*Cylindropharynx*, *Strongylus*). Progressive shortening of the protorhabdions accounts for such forms as *Cylicocyclus*, *Murshidia* and *Oesophagostomum*. Thickening of the protorhabdions and dilation of the protostom account for *Strongylus* and its satellites. Teeth originating at the base of the stoma (lancets) are a common development of the Strongylidae, Syngamidae and Ancylostomatidae. Such onchia are considered products of the telorhabdions. In addition, one often notes a large dorsomedial tooth or a tube in the dorsal wall of the stoma; this tooth or tube is also thought to be a product of the telorhabdions though it may extend to the anterior end of the protostom (*Strongylus*) and is actually the duct of the dorsal esophageal gland. It is often termed the dorsal gutter.

Stomata in the Syngamidae are rather subglobular as in many of the Strongylidae but they differ in that the protorhabdions have six longitudinal thickenings, two medial and four sublateral (*Syngamus*, *Delectocephalus*, *Stephanurus*). In the Diaphanocephalidae (*Kaliocephalus*) the protorhabdions are split sagittally forming a pair of lateral jaws and they usually have four longitudinal thickenings on each side. In addition the telorhabdions form a thick, sclerotized basal plate.

In the Ancylostomatidae the stoma usually has a distinct dorsal bend and is asymmetrically developed as in *Strongylus* due to the large dorsal gutter. In addition there may be either teeth (*Ancylostoma*) or cutting edges developed from the cheilorhabdions on the ventral side.

**Trichostrongyloids** and **metastrongyloids** are both characterized by marked stomatal reduction. Usually there are no distinctly sclerotized stomatal structures. However in a few forms (*Amidostomum*, *Epomidiostomum*-*Trichostrongylidae* and *Stenurus*-*Pseudaliidae*) sclerotized protorhabdions persist to the adult stage. In the Trichostrongyloidea subventral lancets are occasionally present (*Amidostomum*) and the dorsal esophageal gland usually empties into the stoma. In the latter instance its duct often takes the form of a sclerotized onchium which may be the only sclerotized part of the stoma (*Trichoileiperia*, *Haemonchus*). In metastrongyloids teeth of all forms are apparently absent (*Filaropsis*, *Stenurus*, *Dictyocaulus* and *Metastrongylus*). It is interesting to note that trichostrongyloids revert to their ancestral stomatal form, *Rhabditis*, in the first stage larva while metastrongyloids only partially revert in that stage for they have distinct cheilorhabdions and protorhabdions of rhabditoid form but though the mesostom and telostom are recognizable the rhabdions are non-sclerotized.

**ASCARIDINA.** Most ascaridins (Fig. 57) either have a rudimentary stoma or a weakly sclerotized vestibular region but some representatives of the more ancient families, Thelastomatidae and Atractidae preserve a cylindrical rhabditoid stoma. Thus *Leidynema cranifera* and *Probstmayria vivipara* both have stomata in which the various stomatorhabdions are distinctly sclerotized. In *Protrellina* and *Aorurus* of the Thelastomatidae one notes progressive shortening of the stomatorhabdions and loss of sclerotization. The telorhabdions may persist in the form of basal teeth or laminae or they may entirely disappear. The dorsal esophageal gland never empties into the stoma as in the Strongyloidea. In the Atractidae a cylindrical protostom (*Heth*, *Probstmayria*), weakly sclerotized stoma with collapsed mesostom (*Atractis*) and vestibule (*Crossocephalus*) are all known to occur. In the Oxyuridae the protostom is always greatly shortened, often feebly sclerotized (*Enterobius*) but the telorhabdions are commonly large

and conspicuous laminae (*Oxyuris*). The family Rhigonematidae is characterized by a rudimentary stoma surrounded by esophageal tissue (vestibule). The stomatorhabdions are non-sclerotized, with the exception of the cheilorhabdions of *Rhigonema*; these latter take the form of three sclerotized dentate jaws, internal to the lips. In *Icthyocephalus* the stomatal region of the esophagus is horizontally split forming paired jaws.

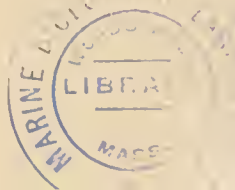
The subfamily Subulurinae of the Ascaridoidea is the only group of that superfamily in which the stomatal region is not surrounded by esophageal tissue. Herein the short heavily sclerotized protostom is followed by a dentate telostom (*Subulura distans*, *Autonocephalus peramelis*) which is strongly reminiscent of *Oxyuris* and *Enterobius*. The other families have weakly or non-sclerotized protorhabdions, the stoma collapsed and of subtriangular or triradiate form in cross section. In the Cosmoceeridae, Kathliniidae and Heterakinae the base of the vestibule (stomatal region of esophagus) is evidenced by a break in esophageal tissue at the original position of the telorhabdions. In the Ascarididae, with the exception of *Crossophorus* there is not the slightest evidence of the original stoma. The esophagus seems to extend uninterrupted to the base of the lips. The single exceptional genus gives the final proof that the anterior end of the esophagus of ascarids is homologous to the vestibule of cosmoceerids and heterakids for in *Crossophorus* there is not only a distinct vestibule but the metastom is dilated and distinct telorhabdions are visible.

**CAMALLANINA.** The first superfamily, Camallanoidea, is characterized by the presence of a well developed stoma in most forms and at least a distinct vestibule in the remainder while the second superfamily, Dracunculoidae, has a rudimentary stoma, the stomatorhabdions are non-sclerotized in all forms (Fig. 58). None of the adults in the Camallanoidea have that which might be termed a rhabditoid stoma but *Procamallanus* most closely approaches it. In this form the stoma is barrel-shaped, cheilorhabdions are not distinct, protorhabdions amalgamated and heavily sclerotized and followed by a transverse ring-shaped telorhabdion. Li (1935) has shown that as in other groups the larva more closely approaches the rhabditoid stoma than does the adult for in the first stage larva the stoma is much more narrow and cylindrical. In adults of other genera of the Camallanidae (*Camallanus sweeti*, *C. americanus*, etc.) the prostom is sagittally slit, forming two lateral jaws; longitudinal ridges of the internal wall of the protostom make their appearance and paired, sclerotized medial tridents are formed at the external surface of the stoma. Somatic muscles are attached to both the tridents and the exterior surfaces of the jaws.

In the Cucullianidae one observes, though not as completely, a repetition of the evolution in the Camallanidae. *Omcia* is the only form which retains the primitive, non-esophageal tissue surrounded stoma but even in this case there is little resemblance to the cylindrical stoma. *Haplonema* and *Scuratum* appear to be products of some genus like *Omcia* in which the stoma collapsed, stomatorhabdions degenerated and were covered with esophageal tissue forming a vestibule. *Cucullanus* may be interpreted as more ancient than *Omcia* in distinct retention of pro- and meso-metarhabdions but less primitive in that the entire stoma is surrounded by esophageal tissue and sagittally divided forming lateral jaws. This is likewise one of the very few exceptional cases wherein esophageal tissue surrounding the stoma is not correlated with stomatorhabdion degeneration.

**SPIRURINA.** Most members of the Spiruroidea (Fig. 58) have a rather cylindrical stoma with strongly sclerotized protorhabdions, but distinct cheilorhabdions are unknown. The stomata of practically all forms are specialized to some extent and none can be regarded as prototypes of the superfamily. However, various members of the Thelaziidae (*Oxyspirura*, *Ascarops*, *Spirocerca* and *Rhabdochona*) indicate that a cylindrical protostom subdivisible into pro- and mesostomata and reduced telostom with plate like telorhabdions were characteristic of the ancestor. One cannot but be struck by the similarity of the stomata of *Longibucca* and *Cylindrogaster* to spirurids both in this respect and in the tendency toward bilaterality in cephalic structures. Nevertheless there is too wide a gap between the Cylindrogasteridae (Fig. 54) and Spirurida for one to assume relationships at the present time.

In a few forms of the Thelaziidae (*Thelazia*, *Pseudofilaria*) the protorhabdions are shortened and amalgamated but in the majority (*Oxyspirura*, *Ascarops*, etc.) the protostom is elongated and there are six onchia at the junction of protostom and mesostom. These onchia may take varied forms, sometimes rounded (*Ascarops*) and sometimes bi- or trifurcate (*Cylicospirura*); in still other instances they may be dentate (*Leuris*) and sometimes opposed by medial plates (*Simondsia*, *Leuris*).



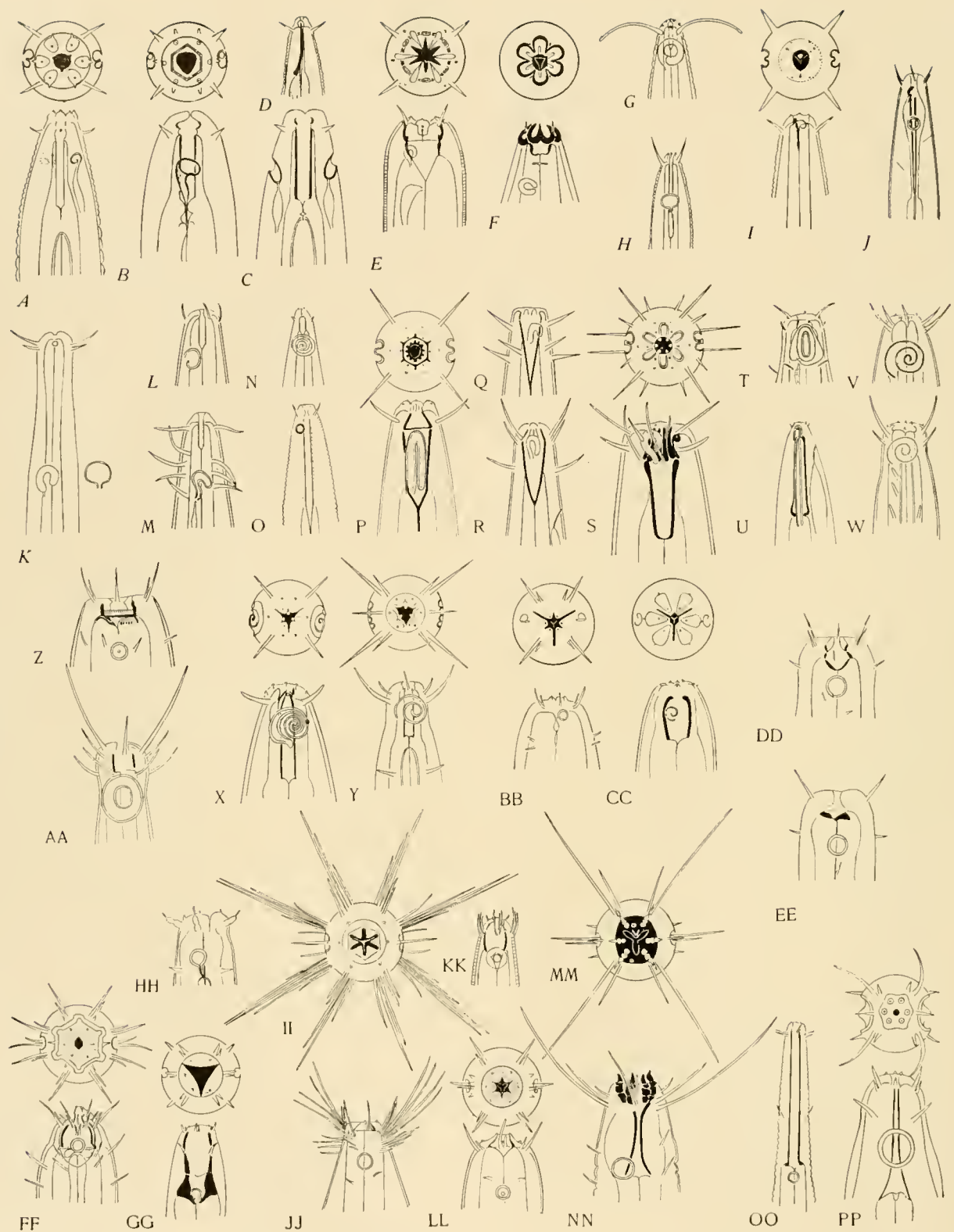


FIG. 60.

Cephalic regions in the Monhysterina. A-C, E-F, H—Plectidae; D, G, I—Camacolaimidae; J-K—Bastianiidae; L-U—Axonolaimidae; V-Y—Comesomatidae; Z-FF—Linhomoeidae; GG-OO—Monhysteridae; PP—Siphonolaimidae. A—*Plectus rhizophilus* (dorsal right); B—*Anaplectus granulosus*; C—*Anaplectus granulosus* (median view); D—*Anguinoides stylosus*; E—*Anaechus mirabilis*; FF—*Teralcephalus cornutus*; G—*Aphanolaimus aquaticus*; H—*Leptolaimus macrinus*; I—*Camacolaimus pytharchi*; J—*Odonatolaimus chlorosus*; K—*Bastiania exilis*; L—*Axanolaimus cylindrolaimus*; M—*Axanolaimus zosterus*; N—*Aegialolaimus elegans*; O—*Cylindrolaimus communis*; P—*Axonolaimus spinosus*; Q—*Axonolaimus odontophoroides*; R—*Axonolaimus subsimilis*; S—*Odontophora angustilaima*?; T—*Didelia maculata*; U—*Pseudobella granulifera* (dorsal right); V—*Sabatieria longicaudata*; W—*Comesoma minimum*; X—*Darglaimopsis metatypicus*; Y—*Laimella quadrisetosa*; Z—*Linhomoeus elongatus*; AA—*Halinema spino-*

*sum*; BB—*Monhysterium transitans*; CC—*Tripylium carcinicola*; DD—*Paralinhomoeus lepturus*; EE—*Metalinhomoeus typicus*; FF—*Sphaerolaimus* sp.; GG—*Halaeonchus macramphidum*; HH—*Cyrtolaimus obtusicaudatus*; II-JJ—*Steineria* sp.; KK—*Omicronema litacium*; LL—*Theristus setosus*; MM-NN—*Scaptocella cincta*; OO—*Rhynchonema cinctum*; PP—*Siphonolaimus* sp. D, H, L, Q, R, GG, HH—After Chitwood, 1936, Proc. Helm. Soc. Wash., v. 3 (1). F—After Cobb, 1914, Tr. Am. Micr. Soc., v. 33, 1—After Chitwood, 1935, Proc. Helm. Soc. Wash., v. 2 (1). J & O—After de Man, 1884, Die frei in der reinen Erde—Nematoden. N—After Stekhoven, 1931, Ztschr. Morph. v. 20 (4). T, U, AA, CC, KK, OO—After Cobb, 1920, Contrib. Sc. Nemat. 9. W—After Chitwood, 1937, Proc. Helm. Soc. Wash., v. 4 (2). Z—After de Man, 1889, Mem. Soc. Zool. France, v. 2. DD-EE—After de Man, 1907, Ibid., v. 20. Remainder original.



Spiral or transverse rugosities of the protostom are confined to the subfamily Asecaropsinae. Similar rugosities are known only in the genus *Pharyngostromyulus* of the Strongylidae. Basal onchia (lancelets) are known only in *Rictularia*, presenting remarkable convergence with the Strongylidae. Careful consideration of the stomatal formation in thelazids is essential to an understanding of the stomata of other spiruroids. The larva of *Physocephalus* has six prostomatal onchia and no lips like the adult *Asecarops*. During later development the circumoral membrane is apparently lost at the same time the prostom is everted. This results in the six prostomatal teeth coming to occupy an external position and they form the basis of two lateral trilobed pseudolabia. The writers interpret the stomata of other families of spiruroids as of this everted type. Later developments of the prorhabdions (pseudolabia) have been discussed with other labial structures.

Members of the Spiruridae tend to have a rather wide, cylindrical well sclerotized mesostom which may become laterally flattened in some genera (*Spirura*, *Protospirura*) but extreme development of pseudolabia and interlabia may obscure the stoma (*Tetrameres* male and *Hedruvis*). Acanthiids are rather uniform in the possession of a long narrow cylindrical mesostom.

Passing to the Gnathostomatidae and Physalopteridae we see the first and only tendency toward vestibule formation in the Spiruroidae. The genera *Spiroxys* and *Hartertia* (Gnathostomatidae) are the only representatives which retain a sclerotized mesostom and in these forms the stoma is much shortened and surrounded by esophageal tissue. *Thubunaca* (Physalopteridae) retains a laterally compressed vestibule while *Physaloptera*, *Abbreviata*, *Skrjabinoptera* (Physalopteridae), *Tanqua* and *Gnathostoma* (Gnathostomatidae) have completely rudimentary stomata, the esophageal tissue proceeding uninterrupted to the base of the pseudolabia. At the anterior end, in such forms, the esophageal lumen becomes dorsoventral before connecting with the labial bases.

The Filarioidea (Fig. 59) might be considered the "astomatous" twin of the Spiruroidae. A few genera, however, are known to have rather distinct, sclerotized stomata. It is interesting to note that such forms are not dissimilar to thelazids. *Desmidocerca* is a striking counterpart for it not only has a cylindrical stoma but also a pair of lateral prostomatal onchia which may be homologous to those of the spiruroids. *Litomosa* has a short stoma practically identical with that of *Thelazia* while *Litomosoidea* has a cylindrical stoma with separate distinct stomato-rhabdions. Even in such forms as *Dirofilaria immitis* one must assume a cylindrical stoma in the not too dim ancestry because such a stoma, although weakly sclerotized, is present in the third stage larva.

## B. APHASMIDIA

As in the Phasmidia, stomatal morphology in the Aphasmidia is of no value as an ordinal character. Forms with a rudimentary stoma occur in each large group and in many of the groups series extend from the cylindroid type, through various modifications ending in instances of convergence.

**MONHYSTERINA.** Members of the Monhysterina (Fig. 60) have one character in common and opposed to the related Chromadorina, namely, that the cheilorhabdions do not take the form of twelve sclerotized longitudinal ridges, (odontia), replacing lips. However, in axonolaimids and monhysterids one may sometimes note a longitudinal sclerotization which is apparently the homologue, or even predecessor of the chromadoroid type.

**Plectoidea.** *Anaplectus granulatus* provides us with the aphasmidian version of *Rhabditis* not only in esophagus and lips but also in the stoma. The cheilostom is hexangular, the protostom, subtriangular in cross section. Cheilorhabdions and prorhabdions are well sclerotized, telorhabdions only faintly sclerotized. *Anaplectus* is unusual in that the protostom has parallel walls; in most plectoids the walls converge posteriorly. In *Leptolaimus maximus* the stoma is extremely long and narrow, prorhabdions distinct while in some related forms the stoma collapses forming a greatly elongate vestibule. *Anonchus mirabilis* and *Teratocephalus cornutus* exemplify shortening and dilation of the stoma with distinct joints at junction of pro- and mesorhabdions. In *Teratocephalus* the prorhabdions are further modified taking the form of six inwardly acting teeth or odontia.

The family Camaeolaimidae is characterized by a diminution in stomata in all forms. In *Aphanolaimus aquaticus* the stoma is minute, cylindroid, with practically non-sclerotized prorhabdions while in *Camaeolaimus pytherchi* only the dorsal stomatal wall is sclerotized and it projects anteriorly as an onchium. *Anguinoides stylosum* is a further example of the

same tendency, in this instance the dorsal onchium is separate throughout its length terminating posteriorly in two knobs. *Anguinoides* is a striking parallel to *Ditylenchus dipsaci* of the Tylenchoidea but we must classify the spear as an onchiostyl in this instance.

Passing to the Bastianiidae, we may judge that the "astomatous" *Bastiania* arose from some such form as *Odontolaimus* which has a greatly elongate, narrow stoma.

Concluding our resumé of the Plectoidea we note that non-muscular esophageal tissue extends beyond the mesorhabdions in such members of the genera *Anaplectus* and *Plectus* as have been studied. Comparing with *Rhabditis*, we would consider this as a more advanced evolutionary development. Such a view is borne out by the somatic musculature of the forms studied. Since there are representatives in the Plectoidea (*Anonchus*), Axonolaimoidea (*Axonolaimus*) and Monhysteroidae (*Halanonchus*) in which esophageal tissue does not extend anteriorly, we must conclude *Anaplectus* while primitive, does not fulfill all obligations of the Aphasmidian ancestor. Combining cephalic characters and general stomatal outline of *Anaplectus* with the more primitive stomatal and somatic muscle characteristics of *Anonchus* we may, perhaps, have the proper picture.

**Axonolaimoidea.** Primarily axonolaimoids have a cylindroid or conoid protostom. In the Axonolaiminae the protostom is conoid, the mesostom surrounded by esophageal tissue; the cheilostom is anteriorly conoid. Thus in *Axonolaimus* we have a close parallel with *Plectus*. Twelve weak longitudinal sclerotizations of the cheilostom are usually evident in *Axonolaimus* species. In *Odontophora angustilaima* these 12 sclerotizations are anteriorly fused forming six large outwardly acting odontia. As we shall later see in dealing with the Chromadorina, the 12 odontia replacing lips in that group probably originated in a form near *Axonolaimus*. The same tendency of the cheilorhabdions, with multiplication of elements may be seen in the Monhysteroidae.

Inconspicuous, weakly sclerotized, cylindroid stomata occur in the subfamily Cylindrolaiminae which includes forms in which esophageal tissue extends to the anterior end of the protostom (*Atracolaimus zosterac*) and forms in which this is not the case (*Cylindrolaimus communis*, *Aegialolaimus degans*). Cylindroid or collapsed stomata occur in representatives of the Campylolaiminae (*Pseudotella granulifera*) and Diplopelatinae (*Didelta maculata*). In the former type the prorhabdions terminate anteriorly in three small teeth, a parallel to *Dorylaimopsis*.

The Comesomatidae have stomata of two general types. In the first the stoma is cylindroid, the prorhabdions are well developed and terminated anteriorly by three equal teeth (*Dorylaimopsis metatypicus* and *Laimella quadrisetosus*); the entire protostom is surrounded by esophageal tissue. In the second, the protostom is collapsed, the rhabdions are non-sclerotized, the esophageal tissue transforms the stomatal region to a vestibule (*Sobatiaria longicaudata*, *Comesoma minimum*). In both instances the cheilorhabdions are short and do not converge anteriorly as in *Axonolaimus*.

**Monhysteroidae.** Stomatal diversity in this superfamily has thus far prevented adequate revision of the group into compact small units. In the majority of instances, when the stomato-rhabdions are well sclerotized esophageal tissue does not surround them (except *Tripylium carenicolum*). We may presume that when the stoma is rudimentary as in *Theristus* or *Cytolaimum*, it reached this condition through shortening rather than vestibule formation and collapse. A few forms with a large conspicuous stoma are retained in this group; such are *Rhynchonema cinctum* with an extremely long cylindroid stoma, *Halanonchus macramphidum*, *Omicranema litorum* and *Sphaerolaimus* sp. with wide, heavily sclerotized stomata. In *Sphaerolaimus* the cheilorhabdions consist of innumerable sclerotized rugae. These same rugae are retained though the protostom has disappeared in *Theristus scotus*, *Steineria* sp. and other typical monhysterids. In *Scaptrella cincta*, on the contrary, one finds the cheilorhabdions transformed into six outwardly acting odontia as in *Odontophora* of the Axonolaimoidea. Many linhomoeids (*Terschellingia pontica*, *Monhysterium transitans*) have no distinctly sclerotized rhabdions and in the remainder one notes degrees in shortening and reduction. Thus in *Linhomocus elongatus* and *Halinema spinosum* the entire stoma is short and wide. In the former one notes subequal cheilorhabdions and prorhabdions with posteriorly converging mesorhabdions. *Paralinhomocus lepturus* and *Metalinhomocus typicus* seem to be further steps in stomatal reduction of this series.

Siphonolaims are a group apart, having the entire protostom transformed into a stomatostyl as in the Tylenchoidea but there is little or no resemblance in the organ itself.

In leaving the Monhysterina, one may note that prostomatal teeth, if present, are anterior, small and subequal. Sometimes a dorsal, anteriad pointing tooth is described in monhysterids. Such a structure is present at the base of the stoma in *Scaptrella*, it is non-sclerotized, and is probably an esophageal development through which the dorsal esophageal gland has its orifice. Heavily sclerotized dorsal teeth do not occur in this group, a distinct contrast with the group to follow.

**CHROMADORINA.** Muscular esophageal tissue always surrounds the protostom in members of this suborder (Fig. 61). Forms with a rudimentary stoma are numerous but they arise through collapse of the protostom rather than shortening. If the protorhabdions are well sclerotized the cheilorhabdions form odontia replacing the lips except in the Tripyloidae. Onehal development is usually apparent, taking the form of a large dorsal tooth opposed by smaller subventral ones.

*Chromadoroidea.* Of this superfamily the Microlaiminae appear to be most primitive from the standpoint of stomatal characters, including, as it does, forms with a subcylindrical protostom and protorhabdions terminated anteriorly by onehia (*Ethmolaimus revaliensis*). In this instance the dorsal onehium is retrorse and the subventrals mere sclerotized oppositional thickenings. In *Statenia trichura* the same structure obtains except that the subventral onehia are also retrorse and but slightly smaller than the dorsal. In *Microlaimus dimorphus* and *Bolbolaimus cobbi* the dorsal onehia assume a mesostoma-

tal position and are axially directed, the smaller subventral onehia being slightly posterior and oppositional in character. In all microlaimids the protorhabdions are moderately sclerotized and completely surrounded by muscular esophageal tissue; the base of the stomatal region is usually indicated by a groove or tissue differentiation. Cheilorhabdions take the form of 12 odontia replacing the lips in function but seldom protruding beyond them.

In the Chromadoridae examples of the same tendencies are evident, *Prochromadora oerleyi* corresponding to *Statenia* and *Odontonema guido-schneideri* to *Bolbolaimus*. In addition the stomatal region may not be set off posteriad (*Chromadora*, *Spilophorella paradoxa*); the prostomatal dorsal onehium in this case may be small or large, the protostom collapsed or apparent. Cheilorhabdions take the form of 12 odontia as in the Microlaimidae.

In the Cyatholaimidae there are two chief stomatal types. In the Cyatholaiminae the cheilorhabdions always take the form of 12 conspicuous odontia which may project anteriorly beyond the labial region (*Pomponema mirabile*); the prostom is wide, meso- and metastom narrow, with converging weakly sclerotized mesorhabdions. A large dorsal axial onehium at the junction of the pro- and mesostomata is usually present and may be opposed by smaller subventral teeth (*Acanthonchus viviparus*). Choanolaims differ in that axial mesostomatal teeth are inconspicuous or absent and the mesostom does

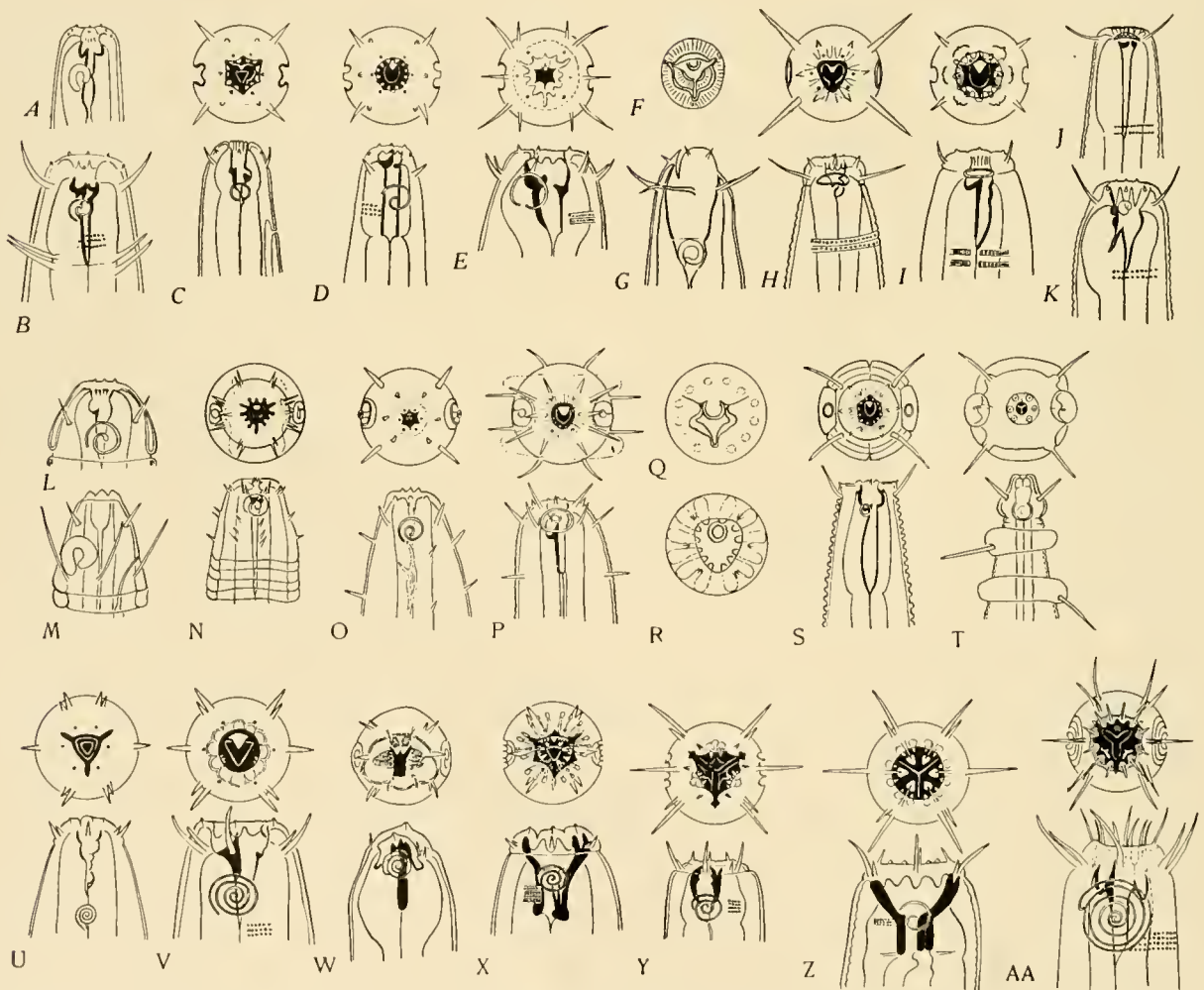


FIG. 61.

Cephalic regions in the Chromadorina. A-F—Microlaimidae. G & U—Tripyloidae. H-K—Chromadoridae. L, N-S—Desmodoridae. M—Epsilonematidae. T—Desmoscolecidae. V-AA—Cyatholaimidae. A—*Achromadora monohystera*; B—*Statenia trichura*; C—*Microlaimus dimorphus*; D—*Ethmolaimus revaliensis*; E—*Bolbolaimus cobbi*; *Bolbolaimus cobbi* (section through stomatal region); G—*Bolbolaimus cobbi*; H—*Chromadora* sp.; I—*Spilophorella paradoxa*; J—*Prochromadora oerleyi*; K—*Odontonema guido-schneideri*; L—*Desmodora scaldensis*; M—*Epsilonematid* (schematic); N—*Croconema mammillatum*; O—*Spirina parasilifera*; P—*Metachromadora onyxoides*; Q—*Metachromadora onyxoides* (stomatal region); R—*Metachromadora onyxoides*

(labial region); S—*Monoposthia heralota*; T—*Desmoscolex americanus*; U—*Tripyloides vulgaris*; V—*Acanthonchus viviparus*; W—*Cheironchus bulbosa*; X—*Halichoanaimus dolichurus*; Y—*Synouchiella truncata*; Z—*Gammanema ferax*; AA—*Pomponema mirabile*. G—After Filipjev, 1922, Act. Inst. Agron. Stauropol., v. 1 (16). J & K—After Filipjev, 1930, Arch. Hydrobiol., v. 20. L—After de Man, 1889, Mem. Soc. Zool. France, v. 2. M—After Steiner, 1930, Deutsche Sudpolar Expedition. N—After Steiner & Hoeppli, 1926, Arch. Schiffsw. Tropenhyg., v. 30. O—After Cobb, 1928, J. Wash. Acad. Sc. W—After Filipjev, 1918, Trav. Lab. Zool. Stat. Bnin. Sebastopol, v. 2 (4). Remainder original.



not have converging walls. In all instances the mesorhabdions are divided into two or more elements to their base. In true choanolaimus (*Halichoanolaimus dolichurus*, *Gammanema ferox*) the prostom is like an inverted cone and the mesostom short, prismatic; cheilorhabdions fuse posteriorly, being continuous with six prostomatal and mesostomatal rugae. Sometimes, in addition, there are numerous denticles at the junctions of pro- and mesorhabdions (*Halichoanolaimus*). On the basis of stomatal characters we should, perhaps, recognize the subfamily Selachinematinae as a valid group of the Cyatholaimidae. While they are undoubtedly closely related to choanolaimus they differ in that cheilorhabdions are feebly developed and the stomatal cavity greatly reduced. The protorhabdions are fused into three or two mandibles terminating anteriorly in several teeth. Of the diverse types, *Synonchiella truncata* seems the most generalized since it has three equal mandibles, one dorsal and two subventral; each of these mandibles is distally bifid and bears several hook-like onchia. *Chironchus bulbosus* exemplifies a partial reduction of the dorsal mandible while *Selachinema ferox* (see cover, Sec. 1, Part 1) represents complete reduction in the dorsal mandible and hypertrophy of the subventrals into lateral jaws.

The Tripyloidea seem misplaced in the Chromodoroida, yet their relationship with the cyatholaims on the basis of other characters makes their position here obligatory. In these forms cheilorhabdions do not take the form of odontia. Instead there are three large lips. Protorhabdions may exhibit numerous joints, the protostom being on the whole inverted, wide conoidal in form (*Tripyloides vulgaris*, *Bathylaimus cobbi*).

*Desmodoroida*. Whenever the protorhabdions are distinctly sclerotized and the protostom not collapsed, desmodoroids (*Metachromadora onyriaides*, *Monoposthia hexalata*, *Desmodora scaldensis*) exhibit all of the characteristics of the Chromadoridae, but quite often the stoma is completely atrophied, in which case protorhabdions cannot be detected (*Ceramonea reticulatum*, Fig. 28). Though axial teeth are present in *Spirina parasitifera* the protorhabdions are feebly developed and cheilorhabdions not apparent.

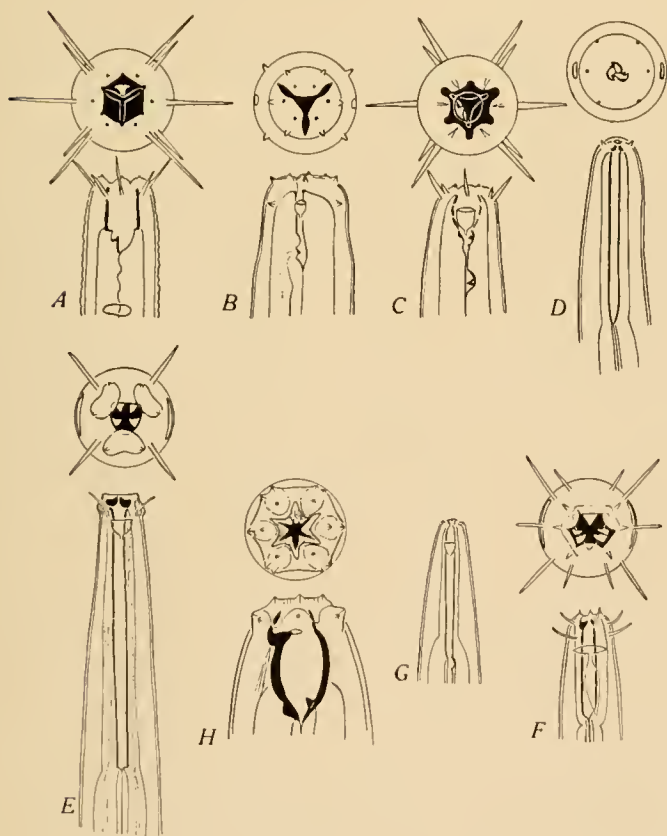


FIG. 62.

Cephalic regions in the Tripyloidea. A-C—Tripylidae. D-G—Ironidae. H—Mononchidae. A—*Prismatolaimus intermedius*. B—*Tripylla* sp. C—*Trilobus longus*. D—*Syringolaimus smaragdus* (upper) and *S. brevicaudatus* (lower). E—*Ironus ignavus*. F—*Cryptochaenus nudus*. G—*Ironella prismatolaima*. H—*Mononchus gertackei*. D—After Cobb, 1928, J. Wash. Acad. Sc., v. 18 (9). H—After de Man, 1904, Expéd. Antarct. Belg. Remainder original.

*Desmoscolocoida*. So far as known, this group must be characterized as having a rudimentary stoma with no visible stomatorhabdions.

*ENOPLINA*. Members of the suborder Enoplina do not have a protrusible onchiostyle and the cheilorhabdions do not take the form of 12 odontia as in the Chromadorina. In a few instances they may form a transverse denticulate ridge. In such instances they do not form an armature of the lips as sometimes occurs in the Monhysterina.

*Tripyloidea* (Fig. 62). Herein are grouped four families, separable on stomatal characters, the Ironidae, with a much elongate narrow stoma and heavily sclerotized protorhabdions, the Alaimidae with a rudimentary stoma, the Mononchidae with a capacious stoma and very heavily sclerotized stomatorhabdions, and the Tripylidae with weakly sclerotized protorhabdions.

Mononchs usually have a subglobular stoma with a massive dorsal prostomatal onchium; the latter may be opposed by a variety of dental structures taking the form of transverse denticulate ridges, longitudinal ventral ridges or small onchia

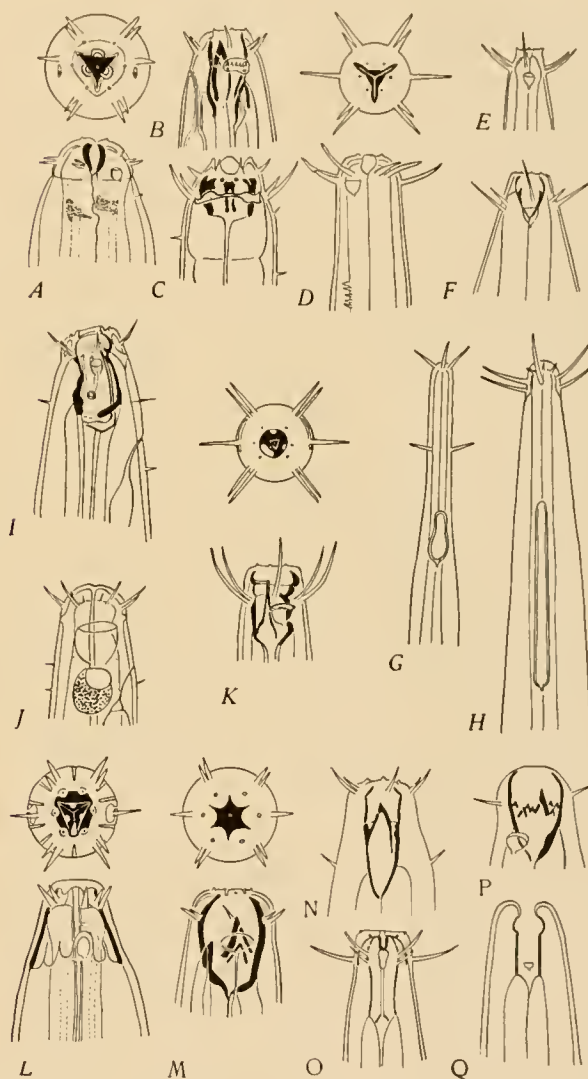


FIG. 63.

Cephalic regions in the Enoploidea. A-F & L—Enopliidae. G-K & M-Q—Oncholaimidae. A—*Enoplius communis*. B—*Eurystomina americana*. C—*Enoploides amphiori*. D—*Anticoma litoris*. E—*Phanodermopsis longistylus*. F—*Rhabdodemania minima*. G—*Orystomina alpha*. H—*Halalaimus carolinensis*. I—*Enchelidium pauli*, v. denticulatum, female. J—*Enchelidium pauli*, v. denticulatum, male. K—*Botbella tenuidens*. L—*Thoracostoma (Pseudocella)* sp. M—*Metoncholaimus pristurus*. N—*Oncholaimellus claudiscus*. O—*Anaplostoma ricparum*. P—*Polyodontus marinus*. Q—*Pseudopelagonema elegans*. B, D, E, F, H—After Chitwood, 1936, Tr. Amer. Micr. Soc., v. 55 (2). C—After Filipjev, 1918, Trav. Lab. Zool. Stat. Biol. Sebastopol, v. 2 (4). I, J—After Micoletzky, 1930, Vid. Medd. fra Dansk. Natur. Foren., v. 87. K—After Cobb, 1920, Contrib. Se. Nemat. 9. N—After de Man, 1890, Mem. Soc. Zool. France, v. 3. O—After de Man, 1907, Mem. Soc. Zool. France, v. 20. P-Q—After Kreis, 1934, Capita Zool., v. 4 (5). Remainder original.

(*Mononchus gerlachii*). *Mononchus tunbridgensis* has all of the family characteristics except that the stoma is of moderate length and cylindroid. Such a form would be the presumptive ancestor of the family.

In the Tripylidae, onchia, if present, are basal. The weakly sclerotized protorhabdions may be many jointed (*Trilobus longus*), or not jointed (*Prismatolaimus intermedius*). The stoma may be subcylindrical (*Prismatolaimus*), conoid (*Trilobus*) or collapsed (*Tripylo*). Dorsal or subventral asymmetrically placed denticles are sometimes present.

In the Ironidae the long subcylindrical to prismoidal stoma is always surrounded by esophageal tissue and sometimes set off as a stomatal swelling (*Ironella prismatolaima*). Except in *Cryptonchus* the cheilorhabdions take the form of outwardly acting odontia (fossors). In *Ironus ignavus* the dorsal odontium is double and the subventrals simple while in *Ironella prismatolaima* the reverse is the case. *Syringolaimus smargidus* and *Dolicholaimus obtusus* have three double equal odontia.

*Enoploidea* (Fig. 63). The families Oncholaimidae and Enopliidae are separable through the fact that only the stomatal base is surrounded by esophageal tissue in the Oncholaimidae while the mesostom and often the prostom is surrounded by muscular esophageal tissue in the Enopliidae.

In the Oncholaiminae the stoma is typically capacious to subglobular, and armed with three unequal conoid mesostomatal onchia which act as orifices of the esophageal glands. One of the subventral onchia usually being the largest (*Metoncholaimus pristiurus*). Sometimes the onchia are multiple (*Polydontus marinus*) and sometimes there is but one, the large subventral (*Oncholaimellus clarodiscus*). A small residue of more primitive species with cylindroid stoma persist as in so many other groups (*Pseudopelagonema elegans*, *Anoplostoma viviparum*).

The subfamilies Eurystominiinae and Euehelidiinae appear as slightly modified oncholaimids. The stoma is more elongate, the stomatorhabdions are usually jointed and the onchia attenuated to a needle-like point. In these groups one subventral onchium is highly developed while the other two are minute if

present (*Bolbella tenuidens*). In addition the cheilorhabdions or prorhabdions may bear minute denticles (*Eurystomina americana*). Sexual dimorphism in stomata makes its appearance in enchelidiids in a most surprising manner. The adult male has a completely rudimentary stoma while the female has a highly developed stoma (*Enchelidium pauli*).

In the Enopliidae stomata are definitely on the wane, being rudimentary in the Oxystominiinae and Phanodermatinae, represented chiefly by three mandibles in Enopliinae and usually quite inconspicuous in the Leptosomatinae. In both, *Enoplus communis* and *Enoploides amphioxii*, the mandibles are the only sclerotized parts of the esophageal lining; these latter are anteriorly bifid and axially hooked. At their bases one finds the three esophageal gland orifices. In some enopliids it is said that small onchia corresponding to those of *Metoncholaimus* are present at the base of the mandibles.

In *Rhabdodemanina minima* (Leptosomatinae) we have an example showing the maximum of stomatal development in the Enopliidae; the prostom is wide, the mesostom conoidal, the walls are moderately sclerotized. Three mesostomatal onchia are present. In other leptosomatids such as *Anticoma litoris* and *Pseudocella* sp. the stoma is completely collapsed and onchia, if present, are minute.

**DORYLAIMINA.** The suborder is characterized by the presence of a protrusible onchiostyl at least in the larval stages. It now seems that this structure persists to the adult stage in many forms in which its presence is not suspected. The group also differs from the Enopliina in that the esophageal glands never empty into the stoma or rudiment thereof.

*Dorylaimoidea* (Fig. 64). Onchiostyls are always well developed and a conspicuous feature of adult dorylaimoids. According to the observations of Thorne (1930, 1935) the onchiostyl originates as a subventral tooth such as one notes in *Nygolaimus brachyuris* or *Sectonema ventralis*. Such an onchiostyl is described as mural. Further development of a ventral groove finally results in a hollow cylinder through which food passes (*Dorylaimus stagnalis*, *Actinolaimus* sp.) in which case the stylet is arial. Evidence of its original formation is

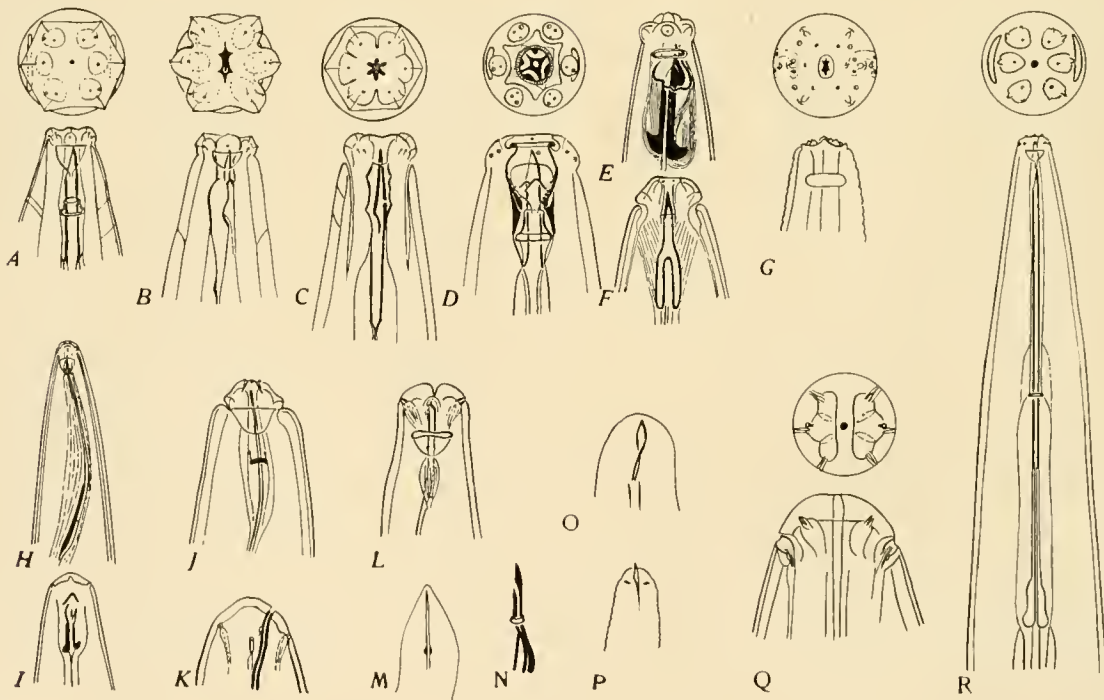


FIG. 64.

Cephalic regions in the Dorylaimina and Dioctophymatina. A-D, F & R—Dorylaimidae. E, H-I—Diphtherophoridae. J—Leptonchidae. G & M—Dioctophymatidae. K-L, N, Q—Mermithidae. O—Trichinellidae. P—Trichuridae. A—*Dorylaimus stagnalis*; B—*Sectonema ventralis*; C—*Nygolaimus brachyuris*; D—*Actinolaimus* sp.; E—*Diphtherophora perplexans* (dorsal view); G—*Eustrangulides ignotus*; H—*Trichodorus obtusus*; I—*Diphtherophora communis*; J—*Trichonchus granulatus*; K—*Eumermis behningi*; L—*Mesomermis bursata*; M—*Dioctophyma renale* (1st stage larva); N—*Mermis subnigrescens* (1st stage larva); O—*Trichinella spiralis* (1st stage larva); P—*Trichosomoides crossicauda* (1st stage larva); Q—*Hexameris albicans*;

R—*Xiphinema americanum*. A—After Thorne & Swanger, 1936, Capita Zool., v. 6 (4). B-C—After Thorne, 1930, J. Agric. Res., v. 41 (6). E & H—After Cobb, 1913, J. Wash. Acad. Sc., v. 3. F—After Cobb, 1918, U. S. D. A., B. P. 1, Agric. Tech. Circ. 1. I—After de Man, 1884, Die frei in der reinen Erde . . . Nematoden. J—After Cobb, 1920, Contrib. Sc. Nemat. 9. K-L—After Steiner, 1929, Zool. Jahrb. Abt. Syst., v. 57. M—After Lukasiak, 1930, Arch. Biol. Soc. Sc. & Lettres Varsovie, v. 3 (3). N—After Cobb, 1926, J. Parasit., v. 13. O-P—After Fuelleborn, 1923, Arch. Schiffs. & Tropenhyg., v. 27. Q—After Rantner, 1906, Zool. Jahrb. Abt. Anat., v. 23. Remainder original.



indicated by the dorsally oblique stylet aperture. It is of further interest to note that in such forms as *Dorylainus* and *Actinolaimus* the stylet is formed as a cylinder in one of the subventral sectors of the esophageal wall; a new stylet moves up to its final position at each molt; while forming, the onchial cylinder has an open crack on the side away from the lumen. Most dorylainids have little evidence of the original proto-rhabdions, these being best preserved in *Nyggolaimus* and *Actinolaimus*. The latter is a most unusual member of the group having a radially striated cheilorhabdion and four massive, onchium-like, stylet guides in addition to heavily sclerotized pro- and mesorhabdions and stylet guiding ring. Since the latter structure is absent in such forms as *Nyggolaimus* we may presume it to be the modified telorhabdions or metarhabdions. However, its homology has not been determined. In dorylainids the stylet may become tremendously elongated (*Trichodorus obtusus*, *Leptonchus granulatus*) and in addition it may be terminated in three flanges (*Tylencholaimus aqualis*) or knobs (*Xiphinema americanum*). In the latter instance we have a case of total convergence with tylenchoids in gross stylet morphology. The guiding ring and oblique stylet aperture provides us with a clue to its dorylain origin. Stylets with flanges or knobs usually show a joint (*Xiphinema*); this joint indicates the extent of the true stylet. The anterior part is the only part formed in the esophageal wall; the posterior part with flanges or knobs, is formed in situ and may be considered a differentiated continuation of the esophageal lining.

The developmental origin and significance of the stylet in *Diphtherophora communis* and *D. perplexans* have not been solved as yet. These forms have a short massive stylet with a complicated dorsal arch at its anterior end and three large knobs at its posterior end.

*Mermithoidea* (Fig. 64). The first stage larva of such mermithoids as *Agamermis decandata*, *Mermis subnigrescens* and *Heramermis albicans* have an onchiostyl quite similar to that of *Dorylainus* and the stoma is completely atrophied. In the adult, as a rule, one can distinguish no semblance of stylet or stoma, and the esophageal lining extends to the oral opening, but in a few forms a very minute stylet rudiment has been described.

*Trichuroidea* (Fig. 64). Fülleborn (1923) showed that the first stage larvae of *Trichuris trichiura*, *Trichinella spiralis* and *Trichosomoides crassicauda* all have distinct stylets. It is customary to assume that all trace of stylet disappears in the adult stage but Li (1933) has found a distinct functional stylet in adult *Trichuris trichiura* and the writers have seen one in adult *Trichuris vulpis*. Such stylets are very difficult to observe in fixed material and should be studied intravital, possibly with the addition of such stains as crystal violet or iodine—1 per cent sulphuric acid. Of all trichuroid stages observed by the writers, the neonate male of *Trichosomoides crassicauda* has a stylet most easily studied.

*Dioctophymatina*. In adult dioctophymatins the stoma is entirely rudimentary; no distinct cavity nor stomatorhabdions can be observed and the esophagus extends to the oral opening. Orifices of three large esophageal glands at the oral opening seem to indicate definite affinities with enoplioids. However, Lukasiak (1930) described a protrusible stylet in the first stage larva of *Dioctophyma renale*. If this observation is verified it will lend additional weight to the trichuroid-dioctophymatoid relationship. Such a relationship was first proposed by Rauter (1918) on the basis of gonads and is supported by the similarity of eggs, spicule and protractor muscles of the spicule.

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## CHAPTER VI

# THE ESOPHAGUS INCLUDING THE ESOPHAGO-INTESTINAL VALVE\*

### 1. GENERAL MORPHOLOGY

The esophagi of nematodes are extremely diverse in both gross anatomy and mode of function; this diversity is correlated with the widely differing feeding habits as well as with the phylogeny of this organ, the result being an assembly of numerous types with examples of convergence and of divergence. In addition features of no apparent present value to the organism are often preserved.

The esophagi of all nematodes have a few characteristics in common, for example their fundamental triradiateness, one ray of the lumen being directed ventrally (though torsion may cause a complete reversal in some regions), a cuticular lining; marginal nuclei and fibers connected with the rays of the lumen or *radii*, radial muscles and nuclei located in the regions between the esophageal *radii*; nerve cells of the esophago-sympathetic system; and glands emptying into the lumen of the esophagus or into the stoma.

The esophagus in cross section has three sectors (Fig. 65), a dorsal sector and two subventral sectors. Cell walls are not distinguishable in the esophagus as a whole; it is, therefore, syncytial. However, the cell walls of nerve cells are usually distinct and the protoplasm of each of the esophageal glands usually retains its identity. The nuclei of the marginal and radial fibers are so placed as to leave no doubt that each belongs to a specific part of the fibers and therefore functions separately.

Through their contraction the radial muscles cause dilation of the esophageal lumen; the marginal fibers are apparently static rather than contractile and the marginal tissue and protoplasm, according to Martini (1908), correspond to the epithelium and form the cuticular lining of the esophagus. The esophagus is often covered externally by a semicuticular membrane which may possibly be a product of the marginal tissue. Longitudinal supporting fibers are usually absent in the esophageal wall. The esophageal glands apparently serve a digestive capacity, the secretion being either ejected through the mouth in case of extracorporeal digestion or passed into the intestine with the food and aiding in intracorporeal digestion. Other possible functions of the esophageal glands will be discussed later.

Nemic esophagi evidence many degrees of cell or nuclear constancy; Looss (1896) first discovered nuclear constancy with reference to the radial, marginal and gland nuclei in ascarids. Since this observation, representatives of the major groups have been studied by us with the result that we find many large groups characterized by a certain number of nuclei of a given type, arranged in a definite manner; loss of nuclear constancy is characteristic of certain groups, and evolution from forms with few cells or nuclei to forms with many cells or nuclei may be traced.

Other points of systematic value in the study of nemic esophagi are: The form of the lumen and esophageal lining, the position of the esophageal gland orifices, the form of the gland ducts and tubules, and finally, the form of the esophago-intestinal valve.

The esophageal lumen itself may be triradiate, the sides of the *radii* converging distally (Fig. 65B), or they may terminate in incomplete tubes (Fig. 65A). In either case the esophageal lining may have thickened *attachment points* at which the radial muscles are inserted (Fig. 65B); whenever the *radii* terminate in marginal tubes, or whenever attachment points are present, the radial muscles are said to be *concentered* (Fig. 65C) while in other instances they are usually dispersed (Fig. 65D).

The dorsal esophageal gland orifice is usually at or near the anterior end of the esophagus. In some cases it is situated on a dorsal tooth projected into the stoma (*Strongylus*, *Ancylostoma*, *Oncholaimus*) but in other cases the orifice is far removed from the anterior end (*Aphelenchoides* *Prionchulus*, *Dorylaimus*). The subventral glands, on the contrary, usually have their orifices in the posterior part of the esophagus (meta-

corpus) and only in rare instances do they extend to the anterior end (Enoploidea, Tripyloidea, Dioctophymatoidea). As a general rule, the duct of an esophageal gland is situated in the middle of a sector and branches are given off into the protoplasm from each side of the central duct. In large forms it has been found that these branches terminate blindly in the form of tubules and the protoplasm is not in direct relation with the lumen. Only the terminal duct is lined with cuticle.

Because of the numerous cases of convergence in gross form, the structural diversity will be discussed group by group uniting both the gross anatomy and the histology in order that evolutionary trends may be more readily observed.

#### A. SUBCLASS PHASMIDIA

All phasmidians have one point in common with respect to the esophagus, namely, the subventral esophageal glands always have orifices far removed from the anterior extremity. On the basis of gross morphology they show no obvious separation into groups but on the basis of histology and developmental anatomy they are divisible into two groups, the orders Rhabditida and Spirurida. In the Rhabditida the esophagus shows evidences, in its larval stages at least, of being composed of two major parts, an elongate corpus and a short bulbar region, while in the Spirurida it is composed of a short muscular anterior part and a long wide glandular part. These are fundamental differences established in the histology of the organ.

**RHABDITINA.** The esophagus of members of the sub-order Rhabditina consists of a cylindroid corpus (further divisible into procorpus and metacorpus\*), a narrow isthmus and a pyriform or elongate bulbar region. In some forms, such as *Rhabditis* (Fig. 65), the bulbar region contains a well developed valve, while in others, such as *Diplogaster* (Fig. 76), no such valve is present. It will suffice for our purposes to describe the esophagus of *Rhabditis* and compare the other forms with it.

The esophageal lumen of *Rhabditis terricola* varies according to the region, the rays of the lumen of the procorpus terminating in well developed marginal "tubes" (Fig. 67a-b), those of the metacorpus in smaller "tubes" and those of the isthmus and bulbar region in acute angles. The lumen is modified at the valve and the lining thickened (Fig. 68c). The procorpus contains 18 nuclei: six radial nuclei ( $r_{1-6}$ ) in one set (RI) near the base of the procorpus, one being on each side of each sector (Fig. 67a-b), and 12 nerve cell nuclei ( $n_{1-12}$ ) arranged in three chains, one in the center of each sector. The radial muscles are concentered in six bands corresponding to the six radial nuclei. The metacorpus (Fig. 66 & 67c-d) contains 28 nuclei: three bilobed marginal nuclei ( $m_{1-3}$ ) in one set (MI)†, six radial nuclei ( $r_{7-12}$ ) in one set (RII), and 19 nerve cell nuclei ( $n_{13-31}$ ) forming three chains as in the procorpus. The isthmus is annulate while the bulb contains 30 nuclei, as follows: six marginal ( $m_{4-6}$ ,  $m_{7-9}$ ), three of which are in the prebulbar region (MII) and three in the postbulbar region (MIH); 12 radial ( $r_{13-18}$ ,  $r_{19-21}$ ,  $r_{22-24}$ ), a set of six of which are in the prebulbar region (RIII) and groups of three in the valvar (R IVa) and postvalvar regions (R IVb); nine nerve cell nuclei ( $n_{32-40}$ ) and three esophageal gland nuclei ( $g_{1-3}$ ). The esophago-intestinal valve has a simple triradiate lumen; its wall consists of an internal layer of transverse fibrous tissue containing two nuclei and an external circular layer containing three nuclei.

The esophagus of *Rhabditis* functions as follows: Contraction of the radial muscles in the procorpus tends to triangulate the lumen thereby increasing its volume; thereafter contraction of the radial muscles of the metacorpus cause dilation of its lumen while relaxation of the muscles of the procorpus and dilation of the bulbar valve occur. In order to discuss the mechanism of the bulbar valve we shall label the parts; the esophageal lining has a series of three thickened regions. During rest the first piece (1) is convex anteriorly while the

\*These terms are substituted for procorpus and postcorpus (p. 10) at the suggestion of Dr. Steiner.

†Not uncommonly the marginal nuclei may appear to be double, in forms with marginal tubes at the termination of esophageal *radii*; in such cases the lobes are designated  $m_{1a}$ ,  $m_{1b}$ , etc.

\*Strictly speaking the esophago-intestinal valve is part of the esophagus. However, in conformity with common usage, the term esophagus as used herein excludes the esophago-intestinal valve unless otherwise specified.



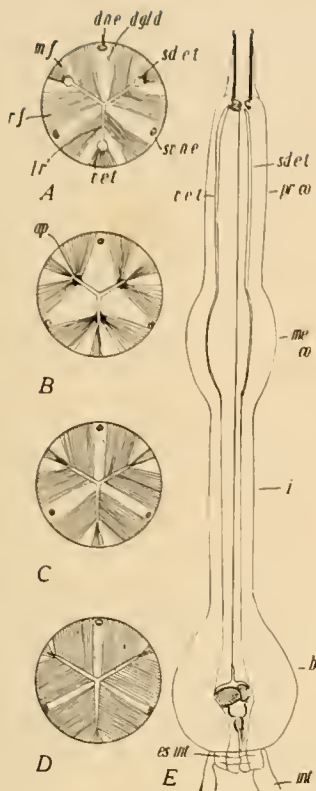


FIG. 65

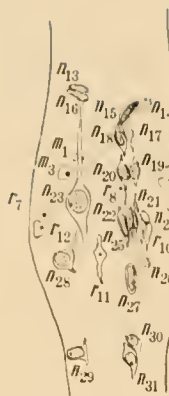


FIG. 66



FIG. 67

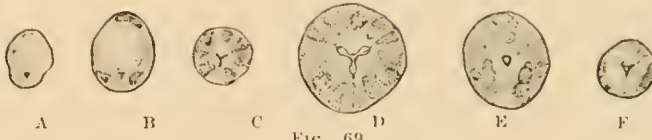


FIG. 69



FIG. 70



FIG. 71

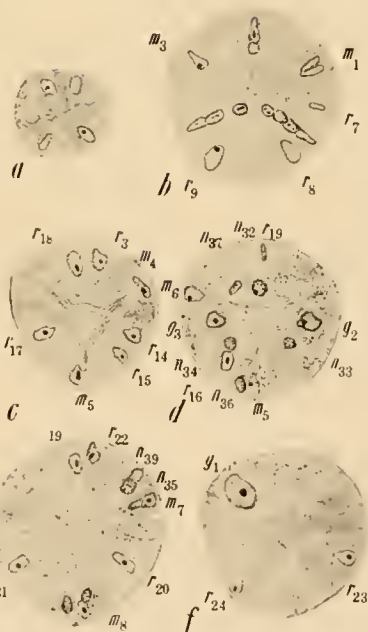


FIG. 68

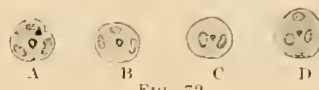


FIG. 72

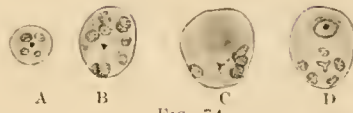


FIG. 73



FIG. 74



FIG. 75

FIG. 65. Diagrams of esophagi. A-D—Cross sections showing various types of muscle arrangement. (A—Radii of esophageal lumen terminated by tubes, musculature concentric; ex. *Rhabditis*, *Leidyneima*, *Heterakis* and first stage strongyles, *Plectus* and *Axonolaimus*; B—Sides of radii converging distally, musculature concentrated, attachment points present; ex. *Oesophagostomum*, *Camallanus*, *Cucullanus*, *Sphaerulimus* and *Metachronandora*; C—Sides of radii converging distally, musculature concentric, no attachment points, ex. *Ethmolaimus*, *Monoposthia*, *Sphulopharella*, *Acanthanchus*; D—Sides of radii parallel, musculature dispersed, ex. *Ascaris*, *Physaloptera*, *Theristus*, *Trippia*). E—Diagram of rhabditid esophagus showing parts of esophagus and relative position of radial tubes of lumen. doe—dorsal esophageal nerve, sv ne subventral esophageal nerve, sd et subdorsal and v et ventral esophageal tubes, mif marginal fibers. lr radius of lumen, ap attachment point, pr co procorpus, me co metacarpus, i isthmus, b bulb. Original.

FIG. 66. Diagram showing nuclei of metacarpus in *Rhabditis*.  
FIG. 67. Diagram showing groups of nuclei in esophagus of *Rhabditis terricola* as occurring in cross section. a-b—Procorpus; c-d—metacarpus; e-f—bulb.  
FIG. 68. *Rhabditis terricola*, esophageal cross sections. a—procorpus; b—metacarpus; c-f—*Rhabditis lamdiensis* bulb.  
FIG. 69. *Ditylenchus dipsaci*. Sections through corpus.  
FIG. 70. *Ditylenchus dipsaci* (Sections through bulbar region).  
FIG. 71. *Ditylenchus dipsaci* (Reconstruction of esophagus with nuclei in position).  
FIGS. 72-75. *Aphelenchus avenae*. 72—procorpus; 73—metacarpus; 74—bulbar region; 75—region of glandular appendage.  
FIGS. 66-75—After Chitw. & Chitw. 1936, J. Wash. Acad. Sc., v. 26 (2); FIG. 65 original.

second and third pieces (2-3) nearly touch one another. Contraction causes a reversal of the position of 1, point *a* (Fig. 97E-F) becoming nearly axial and point *b* moving from an axial position to a point formerly occupied by *a*. This is accomplished by contraction of the radial muscles of the pre-valvar region (associated with  $r_{13-15}$ ) and possibly of the valvar region (associated with  $r_{10-21}$ ). Opposition to this movement, i. e., return to the position of rest, is accomplished by muscles of the valvar region ( $r_{10-21}$ ). Movement of piece 1 to a position of dilation is followed by dilation of the lumen opposite pieces 2-3 in series (through contraction of the post-valvar radial muscles associated with  $r_{22-24}$ ), opening of the esophago-intestinal valve and, finally, closure of this structure. There is no evidence that the marginal fibers are ever contractile. They appear to function entirely in the capacity of "fixed points" upon which the sectors are "hinged." In the corpus, relaxation proceeds slowly while contraction or dilation is spasmodic. Perhaps the tubular form of the esophageal radii contributes to the opposition of the radial muscles because of their elasticity. Muscle fibers definitely opposed by other muscle fibers are found only in the valvar region of the bulb. All muscle fibers of the esophagus are perpendicular or oblique to the esophageal axis; there are no circular or longitudinal fibers.

In *Rhabditis*, the dorsal esophageal gland orifice is at the anterior end of the procorpus (Fig. 76), the short cuticular lined terminal duct is followed by a small ampulla and a long canal extending to the bulb where it becomes lost in the mass of dorsal esophageal gland protoplasm; the canal extends nearly to the base of the bulbar region where the gland nucleus is situated. The subventral gland orifices are situated at the base of the metacarpus and, likewise, each is provided with an ampulla and a canal leading posteriorly to the bulbar region. The mass of the subventral gland protoplasm is lateral in position (i. e., in the lateral part of the subventral sectors) and their nuclei are in the valvar region.

The nerve cells, previously mentioned, form the esophago-sympathetic system which consists of a nerve trunk in the center of each esophageal sector, these trunks being connected by three commissures, one at the base of the corpus, one in the pre-valvar region and one in the post-valvar region. This system is connected with the central nervous system by means of a pair of nerves from the subventral trunks through the external surface of the procorpus.

Other members of the superfamily Rhabditoidea with a valved bulb apparently have the same structure as that described above. In *Diplogaster* (Fig. 76), and similar forms, in which the valve is absent but the radial muscles of the bulbar region not degenerate, slightly larger marginal "tubes" occur in the corpus and the radial muscles associated with  $r_{10-24}$  seem to act together instead of as two separate groups. *Rhabdias* and *Strongyloides* present peculiarities in that the esophagus has a well developed valve in the free-living generation and first stage larva of the parasitic generation, but this structure degenerates in the later development of the parasitic generation though there is no change in the number or arrangement of the esophageal nuclei.

In the superfamily Tylenchoidea, actual degeneration of the radial muscles of the bulbar region takes place but the 30 nuclei of this region which correspond to those in *Rhabditis* still remain (Figs. 70-71). This degeneration of the musculature is correlated with increase in size of the esophageal glands which form practically the entire bulbar region in forms such as *Ditylenchus dipsaci* and may even extend beyond the base of the esophagus as one or more esophageal appendages as in *Aphelenchus avenae* (Figs. 75-76). In a few forms, such as *Aphelenchus* and *Aphelenchoides*, Cobb (1923) showed that the dorsal gland orifice is situated in the anterior part of the metacarpus instead of the anterior part of the procorpus as is generally the case. In many tylenchids the metacarpus is unusually large and acts as the chief "pump" of the esophagus, while in the Allantonematidae the musculature of the entire esophagus appears degenerate.

**STRONGYLINA.**—Members of the suborder Strongylina have an esophagus which is grossly clavate to cylindroid but in some instances faint indications of procorpus, metacarpus, and bulbar region are observable in the adult. The first stage larvae of strongyloids and many trichostrongyloids have an esophagus identical with that of *Rhabditis*; during the second and third stages the esophagus becomes more elongate and the valves of the bulbar region disappear resulting in an esophagus reminiscent of that of *Diplogaster* except that the metacarpus is not enlarged or as distinctly set off. With progressive development the various regions become grossly obliterated to a greater or lesser degree. Metastrongyloids differ from strongyloids and most trichostrongyloids in that first

stage larva does not have a valved bulb, but more closely corresponds in its morphology to the second and third stage larvae of the other two superfamilies.

The detailed structure of the esophagi of strongylins was studied by Jägerskiöld (1897), Looss (1905), Imminck (1921, 1924) and the writers (1934, 1935). It was found that the marginal, radial, and gland nuclei agree in number with those of *Rhabditis* but the pre-valvar radial nuclei ( $r_{13-15}$ ) are arranged in two groups of three nuclei each, near the center of the sectors. There is no essential difference in arrangement of the nerve cells though there is considerable variation as to the total number observed (from 29 in *Metastrongylus elongatus* to 44 in *Strongylus edentatus*). The triradial esophago-intestinal valve seems to be composed of seven cells. The sub-ventral esophageal gland nuclei are quite minute in members of the Strongyloidea and thus far gland orifices near the nerve ring have been observed but rarely. This may be correlated with the hypertrophy of the dorsal gland characteristic in such forms, and it may have a distinct bearing on the feeding habits.

The musculature is always "concentered" rather than "dispersed" in strongylins, and the lumen may have marginal tubes as in *Metastrongylus* or there may be a series of thickenings of the esophageal lining forming attachment points as in *Oesophagostomum dentatum* (Fig. 78) and *Ancylostoma duodenale*.

**ASCARIDINA.**—More work has been done on the esophagi of representatives of the suborder Ascaridina than of representatives of other groups. It was in *Parascaris equorum* that the orifices of esophageal glands were observed for the first time in any nematode by A. Schneider (1866). Subsequent work has been carried out by Jägerskiöld (1893, 1894), Hamann (1895), Looss (1896), Ehlers (1899), Jerke (1901), K. C. Schneider (1902), Goldschmidt (1904, 1909, 1910), Martini (1916, 1922), Kulmatycki (1918, 1922), Allgen (1921), Mueller (1929, 1931), Hsu (1929, 1933), Plenk (1924, 1925, 1926), Chitwood (1931), Chitwood and Hill (1931), Chitwood and Chitwood (1933, 1934, 1936), de Bruyn (1934), and Mackin (1936).

In ascaridins the esophagus varies in gross morphology more than in any other group. The members of the superfamily Oxyuroidea are less diverse in detailed anatomy than are the members of the superfamily Ascaridoidea. In the former group, the esophagus in the adult stage is basically rhabditoid, having, with a few questionable exceptions, a cylindroid corpus, a more or less distinct isthmus, and a valved bulb. In numerous forms, such as *Syphacia* and *Oxyuris*, the corpus may be clavate while in a few, such as *Ransomnema*, it may be fusiform. In some forms the metacarpus is enlarged and either cylindroid as in *Leidynema* or ovoid as in *Hammerschmidtella*; in odd types the entire corpus is pyriform (*Aorurus*) and in still others the procorpus only is fusiform (*Ozotaimus*). The isthmus also is diverse in gross appearance, sometimes being greatly elongated as in *Atractis* or *Aorurus*, sometimes only moderate in size as in *Thelastoma*, sometimes recognizable only as a groove as in *Rhigonema* and sometimes subglobular as in *Labidurus*. Less diversity occurs in regard to the bulb; it is valved except in a few genera such as *Dermatomyx* and *Leiperenia* but the degree of development of the valves differs greatly between the typical rhabditoid form of *Thelastoma* and the much reduced type of *Oxyuris*.

One would presume that forms such as *Leidynema* (Fig. 76) and *Hammerschmidtella* represent the primitive type since the metacarpus is enlarged as in *Rhabditis* and since careful study proves the corpus to be subdivided into pro- and metacarpus even in forms in which these parts otherwise are not grossly separable. However, primitivity apparently does not apply here since in the genera *Leidynema* and *Hammerschmidtella* the esophagus does not reach this stage of development until adulthood of the female. The juvenile females, as well as the adult neotenic males, have a cylindrical corpus as in *Thelastoma*. Sexual dimorphism in the esophagus as well as cephalic structures, stomata, and cuticular ornamentation is one of the outstanding oddities of the Thelastomatidae and Ransomnematinae. Developmental modifications, without apparent bearing on relationship, have also been described in *Oxyuris equi* by Ihle and Van Oordt (1921) and Wetzel (1930); in this species the fourth stage larva has a pseudostom formed by the dilation of the entire corpus (Fig. 97 O).

In their detailed anatomy, the oxyuroids show less diversity. The lumen of the corpus usually shows the marginal "tubes" as in *Rhabditis* and sometimes in addition (or sometimes instead of them) the esophageal lining has distinct cuticular thickenings or attachment points for the radial muscles. The three esophageal glands (some statements to the contrary) open as in *Rhabditis*, i. e., the dorsal near the base of the



stoma, the subventrals near the base of the metacarpus. The number and arrangement of the nuclei corresponds totally or approximately to *Rhabditis* in all forms studied with one exception: Martini (1916) records three nuclei in each of the subventral esophageal glands of *Oxyuris equi* which fact might conceivably be due to either gigantism or misinterpretation. The esophago-intestinal valve is triradiate, more or less rhabditoid, and contains five to seven nuclei.

The Ascaridoidea includes some forms which have esophagi of the thelastomatid type such as *Cosmocercoides*. With the

exception of the Ascarididae (in which no indication of a stomatal region is apparent) and the Subulurinae (in which there is a short wide stoma) the stomatal region in the Ascaridoidea is surrounded by esophageal tissue containing radial muscle. The modified stomatal region so formed is termed a *vestibule*. In some ascaridoids, the isthmus is obliterated, the bulb being in direct continuity with the corpus such as *Heterakis*, while in still others (*Spironoura*), it may be ovoid to spheroid; a few forms have no valves, the bulbar region being elongated (*Quimperia*) and others have a cylindrical esophagus either

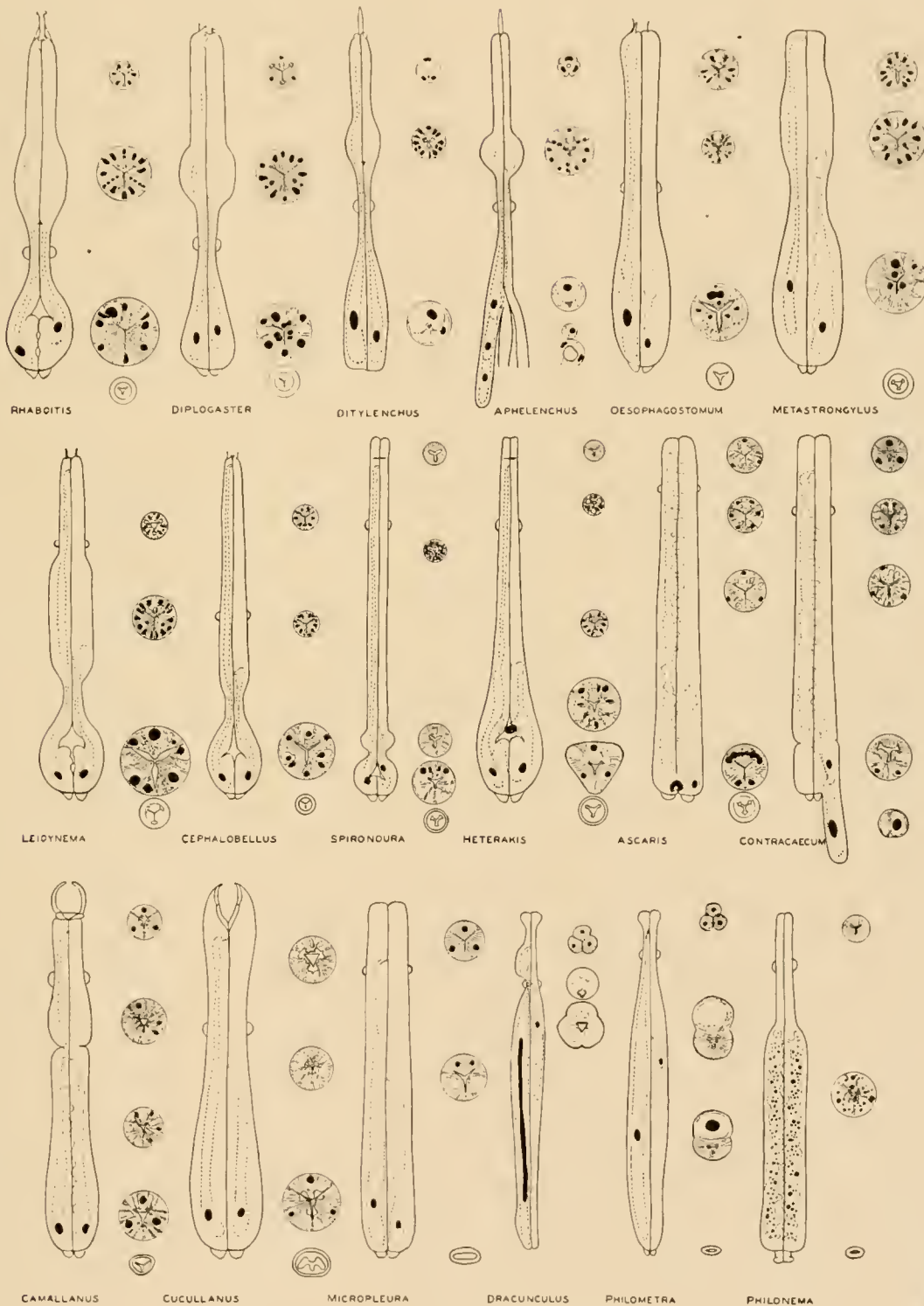


FIG. 76

Diagrams of esophagi, including representatives of the Rhabditoidea (*Rhabditis*, *Diplogaster*), Tylenchoidea (*Ditylenchus*, *Aphelenchus*), Strongyloidea (*Oesophagostomum*), Metastrongyloidea (*Metastrongylus*), Oxyuroidea

(*Leidynema*, *Cephalobellus*), Ascaridoidea (*Spironoura* to *Contracaecum*), Camallaboidea (*Camallanus*, *Cucullanus*), Dracunculoidea (*Micropleura* to *Philonema*). Original.



with or without a distinctly set off bulbar region (*Ascaridia* and *Ascaris*, *Torocara* and *Contracacum*, etc.). It is in the latter group that we have the outstanding diversity of the superfamily. While the bulbar region is always distinct in the larva when removed from the egg it may totally disappear from the standpoint of gross examination during later stages in its development (*Ascaridia*, *Ascaris*, *Torascaris*, etc.). In other forms it remains grossly unmodified but becomes relatively smaller due to the disproportionate increase in length of the corpus (*Torocara*) and in some it becomes elongated forming a short cylindroid glandular region (*Anisakis*). Forms which retain a bulbar region often have one or more posteriorly directed bulbar appendages (*Contracacum*, *Multicacum*). The internal structure varies fully as much as the gross appearance and its variations will be dealt with separately.

Ascaridoids with a valved bulb invariably have marginal

"tubes" in the region of the corpus and concentrated radial fibers but the esophageal lining is without thickened attachment points in all forms.

Meromyarian forms such as cosmoceroids and kathlaniids have approximately the same nuclei as are present in rhabditoids and oxyuroids (one group of three large marginals and two groups of six large radials in the corpus; two groups of three marginals, one group of six radial and two groups of three radials, and three gland nuclei in the bulb). Polymyarian forms, such as heterakids and ascaridids show evidence of additional cell division in the esophagus, for in heterakids there is an additional group of six radial nuclei in the procorpus making a total of 30 radials and the subventral esophageal glands are each binucleate. In ascarids there are 36 radials and 12 marginals, the additional nuclei (six radials and three marginals) being situated anterior to or opposite the orifice

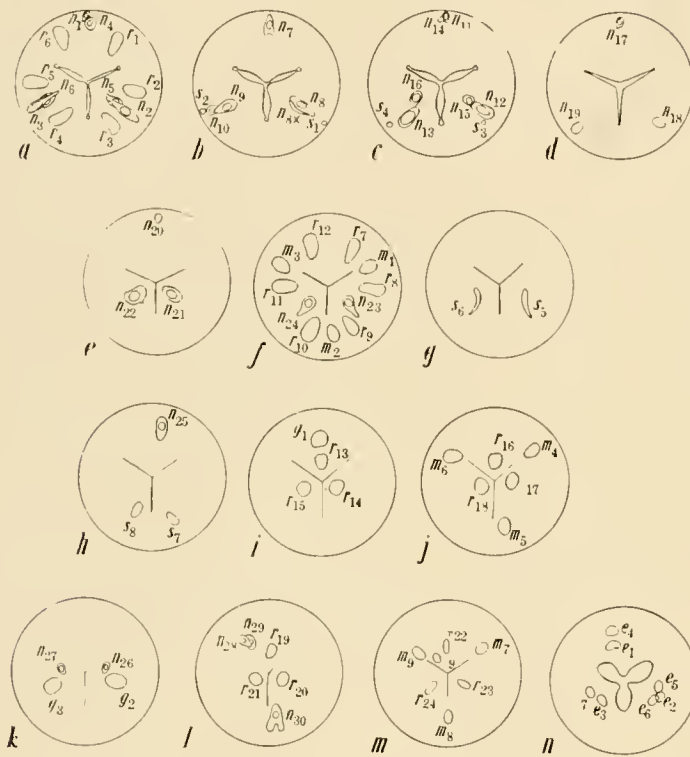


FIG. 77

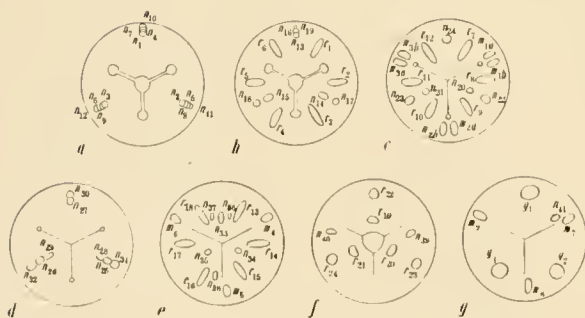


FIG. 79



FIG. 80

FIGS. 77-80

Diagrams showing distribution of nuclei in the esophagi of *Metastrongylus elongatus* (77), *Oesophagostomum dentatum* (78), *Leidy-nema appendiculatum* (79), and *Heterakis gallinae* (80). After Chitw. & Chitw., J. Wash. Acad. Sc.



of the dorsal esophageal gland. The anterior radials (Fig. 81) in this case are located in the center of their sectors, in two groups of three, the remaining radial groups of the corpus are broken, i. e., each group of six is subdivided into two groups of three, one in each sector and these nuclei may or may not become centrally located according to the particular genus. Members of the Ascarididae have only three esophageal gland nuclei and for that reason *Ascaridia*, with binucleate subventral glands, though the esophagus is cylindrical, must be placed in the Heterakidae.

Whether or not the esophagus retains its gross separation into corpus and bulbar regions in the adult, the two regions are histologically separable the base of the corpus being indicated by the basal commissure of the metacarpus. In ascaridids the esophageal glands undergo many peculiar modifications (see Hsu, 1929, 1933). The dorsal gland situated near the base of the bulbar region is bilobed in *Ascaris lumbricoides* the lobes are marginal and connected by a fine strand. In this form lobes of the dorsal gland extend into the subventral sectors of the corpus giving the appearance of fusion of tissues. However, in such forms the subventral glands do not extend into the anterior part of the esophagus. According to Hsu, 1933, the dorsal gland nucleus completely surrounds the esophageal lumen in *Anisakis* and becomes ventrally situated in *Toxocara* and *Contracaecum*. Thus, though the ventrally situated bulbar appendage in *Contracaecum* represents the two subventral sectors of the esophagus and may or may not contain small lobes of the subventral esophageal glands, it is chiefly formed by the much enlarged dorsal gland (Fig. 76).

have arisen. There are two superfamilies, Camallanoidea and Dracunoidea, the former being characterized by relatively well developed musculature usually having cuticular attachment points for the radial muscles and an esophago-intestinal valve that is either triradiate or shows reminiscences of this condition, while the latter group has enormously developed esophageal glands, relatively meager musculature in the glandular region, no attachment points and a dorso ventrally flattened esophago-intestinal valve.

Esophagi of Camallanoids have been studied by Jägerskiöld (1909), Magath (1919), Törnquist (1931), and Hsu (1933). *Camallanus microcephalus* has a so-called "divided" esophagus (Figs. 76 & 98 E-F). Here the dorsal gland orifice is somewhat posterior to the base of the stoma, the subventral gland orifices at the anterior end of the posterior part of the esophagus. In the anterior part of the esophagus there are 18 radial nuclei and six marginal nuclei, the radials in four groups, two groups of three anterior to the dorsal gland orifice and two groups of six posterior to this level; the marginals are in two groups, one situated near the level of the dorsal gland orifice, the other between the third and fourth radial groups. In the posterior part of the esophagus there are likewise 18 radials in four groups and six marginals in two groups. Here the first group of six radials is situated near the anterior end of this part of the esophagus at the level of the subventral gland orifices, the second group of six radials somewhat anterior to the mid region of this part, and the third and fourth groups of three radials near the base of the esophagus. One marginal group is just posterior to the level of the subventral gland orifices



FIG. 81

Tables of esophageal nuclear distribution of Phasmodians. Original.

**SPIRURIDA.**—The essentially different form of the esophagus in the order Spirurida has been previously mentioned. The fact that the esophagus is always histologically divisible into a short muscular anterior part and a long glandular posterior part is not of course, noticeable in many forms with cylindrical or even clavate esophagi. However, the fundamental significance of this type of organization is evidenced by the absence of any stages in the life history showing reminiscences of the rhabditoid esophagus such as were mentioned for the Strongylina and Ascaridina.

**CAMALLANINA.**—The suborder Camallanina contains forms in which the esophageal glands are primarily uninnucleate; secondarily a few forms with multinucleate glands appear to

while the other is near the level of the third group of radials. It would appear obvious from the nuclear distribution (Fig. 81) that the posterior or glandular region corresponds not only to the bulbar region of *Rhabditis* or *Ascaris* but also to the metacarpus of *Rhabditis* and part of the metacarpus region of *Ascaris*, since the bulbar region in these forms contains only six marginal and 12 radial nuclei while the posterior part of *Camallanus* contains 18 radial and six marginal nuclei. This view is supported by the fact that the commissure of the metacarpus is situated in the anterior part of the glandular region of the esophagus of *Camallanus*.

In *Cucullianus* though the esophagus is clavate instead of being divided (Fig. 76) we observed essentially the same

nuclear arrangement and gland orifice positions in the posterior swollen region. The nuclei correspond to those of the posterior part of the camallanid esophagus.

Esophagi of dracunculoids were studied by Jägerskiöld (1894), zur Strassen (1907), Mirza (1929), Hsü (1933), and Yamaguti (1935). In gross features the esophagus may be cylindrical as in *Micropleura*, clavate or fusiform as in *Philometra*, divided into a short narrow anterior muscular part and a long wide posterior glandular part as in *Philonema*, *Dracunculus* and *Avioserpens*. In *Dracunculus* and *Avioserpens* the glandular region is constricted in the latitude of the nerve ring (Fig. 76). In *Dracunculus*, *Avioserpens* and *Philometra*

the anterior end of the esophagus takes the form of a sub-globular swelling but does not do so in *Philonema* and *Micropleura*.

The radial and marginal nuclei in *Dracunculus*, *Avioserpens* and *Micropleura* follow the same arrangement as in *Camallanus*, R I and R VI being divided groups. All these nuclei are also in the same position relative to the level of the orifice of the esophageal glands. In *Dracunculus* and *Avioserpens* the region posterior to the constriction at the nerve ring corresponds to the posterior part of the esophagus of *Camallanus*; in the two former genera an additional peculiarity is observed; the dorsal esophageal gland and its nucleus are tremendously enlarged

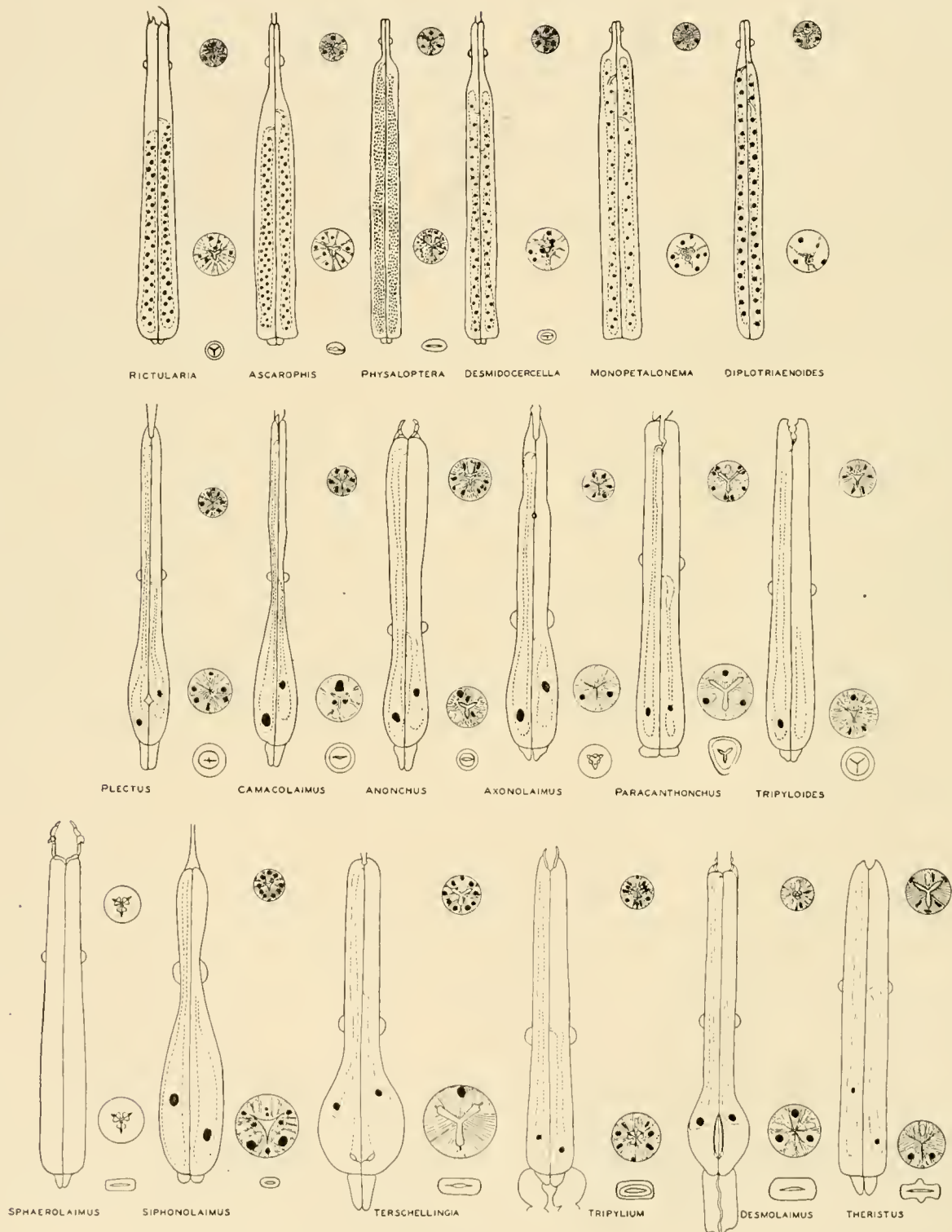


FIG. 82

Diagrams of esophagi; including representatives of the Spiruroida (*Rictularia* to *Physaloptera*), Filarioidea (*Desmido-cer-cella* to *Diplo-tri-ae-noides*), Plectoidea (*Plectus* to *Anon-*

*chus*), Axonolaimoidea (*Axonolaimus*), Chromadoroidea (*Para-canth-on-chus*, *Tripyloides*), Monhyseroidea (*Sphaerolaimus* to *Theristus*). Original.



(Fig. 81). In *Philometra* the fourth and fifth groups of radial nuclei (R IV and R V) are also divided into two subgroups each, but the marginals and radials retain the same relative positions as in *Dracunculus*; however, in the latter the subventral glands (Fig. 76) are greatly reduced in size. Yamaguti (1935) described a genus, *Lethyofilaria*, with a posterior glandular appendage similar to that observed in *Contraecacum*. However a study of the histology of this structure has not been made.

*Philonema* represents the ultimate in esophageal gland development of the Draconuloidea. This genus has the typical spiruroid-filarioid esophagus, a fact that opens the question whether or not it is correctly placed in the suborder Camallanina. All three esophageal gland orifices are located in the posterior, much enlarged glandular region of the esophagus and the esophageal glands are multinucleate. The radial nuclei of all six groups are arranged in triplets, i. e., all six groups are subdivided; since there are three groups of radials in the anterior muscular part of the esophagus one would judge this part to be homologous to the anterior portion of the esophagus of *Camallanus*; the position of the subventral gland orifices (Fig. 76) is in support of this view. The dorsal gland orifice is shifted considerably posterior in this form. The esophageal glands each contain several hundred nuclei of varying sizes often arranged in apparent "constellations" such as one would expect from nuclear budding induced by gigantism. Perhaps this case is analogous rather than homologous to that of the multinucleate glands of spiruroids. In the spiruroids the many gland nuclei apparently arose through typical division because they are approximately equal in size. If *Philonema* did arise separately the gigantism of these glands in *Dracunculus* and *Philometra* might be correlated with the unequal nuclear divisions (amitosis?) in the gland of *Philonema*.

**SPIRURINA.**—There are two esophageal features common to the forms contained in the suborder Spirurina, namely, that the esophageal glands are always multinucleate and that the dorsal gland always opens in the glandular (posterior) part. Esophagi of members of this group are grossly cylindrical or divided into a short anterior muscular part and a wide posterior glandular part. Even in forms with a cylindrical esophagus these two parts are distinguishable on the basis of their consistency. The gross form of the esophagus appears to be of no phylogenetic significance since changes from distinctly "divided esophagi" to cylindrical esophagi occur sporadically within groups of closely related genera.

In all except one family the marginal and radial nuclei are of the same number as in the suborder Camallanina (totals of 12 and 36 respectively); in this one exceptional family, the Physalopteridae, there appears to be a non-limited number of radial nuclei (Fig. 81); the radial nuclear sets usually are all subdivided, three in each group, but in some forms (Fig. 81) the second, third or fourth may be partially or not at all subdivided. Regardless of the gross apparent extent of the glandular region, in all forms the anterior muscular part contains only the first 12 radial nuclei and the posterior glandular part contains 24 radial nuclei (or more as in *Physaloptera marillaris*); the anterior part does not, therefore, correspond to the entire anterior part of the esophagus of *Camallanus*. Since the fifth and sixth groups of radial nuclei of *Camallanus* appear to correspond to the radial nuclei of the bulb of *Rhabditis* and the fifth and sixth groups of *Ascaris*, one would conclude that the remainder of the esophageal nuclei are homologous to those of the corpus; since the second group of marginal nuclei is typically anterior to or opposite the third group of radial nuclei, the third and fourth groups of radial nuclei of *Camallanus* are probably homologous to the second group of radial nuclei of *Rhabditis* which has divided in this form; hence the second group of marginal nuclei and third and fourth groups of radial nuclei are homologous to the metacarpus; if, likewise, the first group of radial nuclei of *Rhabditis* divided as also the first group of marginal nuclei of this form (the marginals migrating anteriorly) then the homologies indicate that whatever region contains the first and second group of radial nuclei in a spiruroid is the procorpus. Therefore, we may say with a reasonable degree of certainty that the anterior muscular region of these forms is the procorpus and the posterior glandular region is metacarpus and bulbar region.

The esophageal glands of spiruroids and filarioids have very many nuclei, varying from a minimum of about 30 each to a maximum that can scarcely be estimated in forms such as *Physaloptera*. The increase in nuclear number in these forms has apparently progressed with regularity in division since the nuclei are fairly equal in size.

The esophageal lumen may be simple-triradiate as in *Rictularia coloradiensis* (Fig. 82), somewhat dilated but convergent peripherally as in *Ascarophis* or contain marginal "tubes" as in *Dermidocerca numidica* and *Diplotriacnoides* (Fig. 82). Furthermore the esophageal lining may have thickened regions as in *Monopetalonema physalorum*, sometimes with distinct attachment points, or it may be unmodified. Thus far the possible phylogenetic significance of such structures has not been determined but modifications appear to be most pronounced in the forms found in body cavities or tissues, i. e., Filarioidea. The form of the esophago-intestinal valve changes from a distinctly triradiate shape such as is found in *Rictularia* to a dorsoventrally flattened structure such as is found in *Physaloptera*.

Further information on nuclear arrangement, esophageal lining and shape of lumen and esophago-intestinal valve, will result in substantial evidence bearing on the inter-relationship of members of the suborder Spirurina.

## B. SUBCLASS APHASMIDIA

Aphasmidians as a whole have no single esophageal feature in common. Like the subclass Phasmodia they are divisible into two major groups on the basis of the esophagus, the first order, Chromadorida, corresponding to the order Rhabditida, contains forms in which the esophagus is primarily divisible into corpus, and bulbar region, the second order, the Enoplida, contains forms in which this division is not grossly apparent.

**CHROMADORIDA.**—The esophagi of members of this order have three uninucleate esophageal glands; the dorsal gland orifice is situated at or near the base of the stomatal region (never, so far as is known, does the gland empty directly into the stoma through a tooth); the subventral gland orifices are at the base of the corpus. Representatives of this order have been studied by the writers (1936).

The suborder Monhysterina contains forms in which the esophago-intestinal valve is relatively well developed, often quite elongated, and dorso-ventrally flattened, or rounded rather than triradiate.

Of the whole Aphasmodia the representatives of the superfamily Plectoidea most closely approach the Rhabditoidea, for in this group forms such as *Plectus* have a rhabditoid esophagus with a well developed valve in the bulb, but unlike *Rhabditis* the pro- and metacarpus are seldom apparent on gross study. The lumen of the corpus terminates marginally in distinct tubes and the valve of the bulb works in a manner similar to that of *Rhabditis*. Other plectoids have an elongated bulbar region without valves and in some forms the corpus also may be quite elongate (*Leptodaimus*), while in others (*Anonchus*), the entire esophagus may be cylindrical (Fig. 82). The musculature of the bulbar region may be reduced so that this region forms an elongate glandular swelling (*Camacolaimus*, *Anguinoides*, *Aphanolaimus*) similar to that part of the esophagus of *Ditylenchus*, and in still other forms such as *Onchium ocellatum* the esophageal glands may project posteriorly beyond the base of the esophagus. It would appear, therefore, that not only in stylet and stomatal formation but also in esophageal formation the Plectoidea present a parallel series to the Rhabditina. In two points all plectoids are similar, the esophageal lumen of the corpus peripherally is terminated by marginal tubes and the esophago-intestinal valve is definitely dorso-ventral in symmetry (Figs. 83-84).

The corpus of all forms contains four groups of six radial nuclei (24) and two groups of three (or three double) marginal nuclei (total 6 or 12). The radial muscles of the corpus are more or less concentrated but no forms are thus far known in which the lining is thickened forming attachment points. As in *Rhabditis* in the bulbar region there are 12 radial and 6 (or 12) marginal nuclei, the first set of 6 radials and the first set of marginals forming the prevulvar region; the succeeding radials are arranged in two groups of three which together with the second set of marginals form the post-vulvar region. In *Anaplectus granulatus* (Fig. 83) and similar forms with unusually well developed "tubes" at the ends of the esophageal radii the marginal nuclei of each group are double, one member of each pair being on each side of each tube, while in forms such as *Camacolaimus prytherchi* in which the tubes are minute (Fig. 84), no such doubling of marginal nuclei occurs.

Representatives of the superfamily Axonolaimoidea have esophagi like plectoids except that no representative of this group has a valved bulb and no forms are known in which the bulbar region is principally glandular through enlargement of esophageal glands at expense of muscular tissue (Figs. 82 & 84). The entire esophagus may be clavate (*Comesoma*, *Sabatia-*



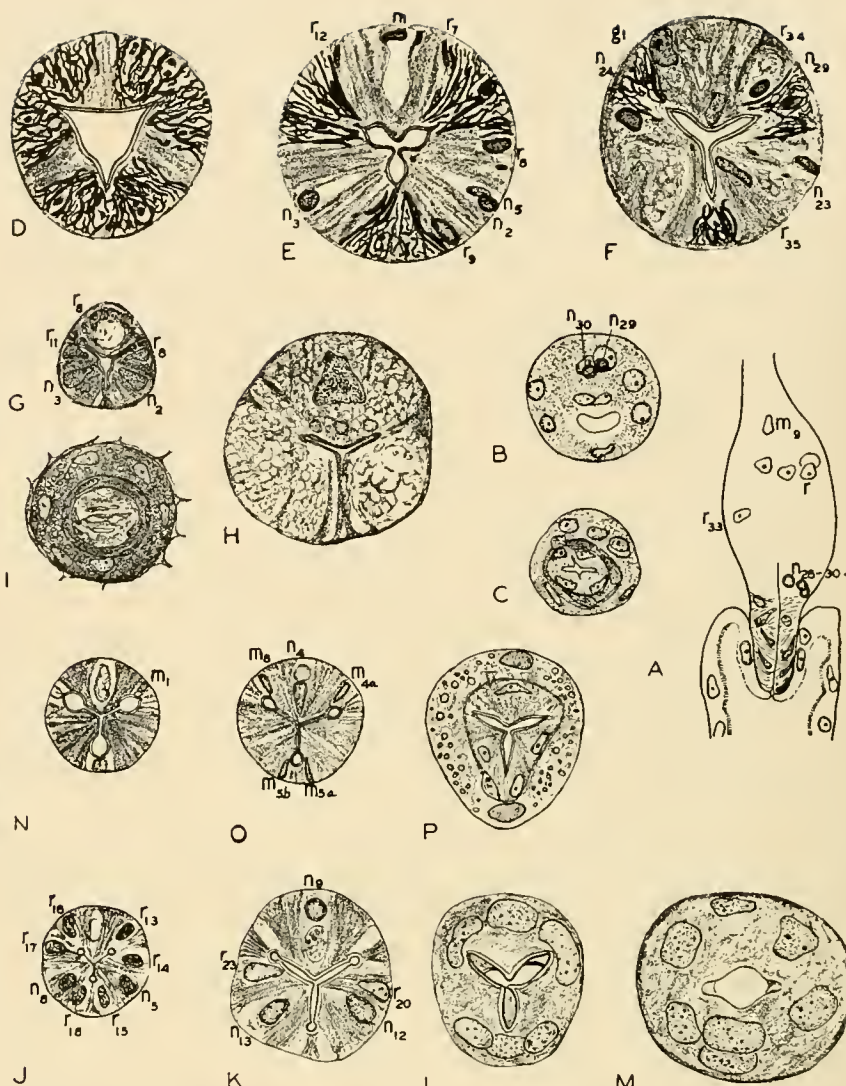


FIG. 84

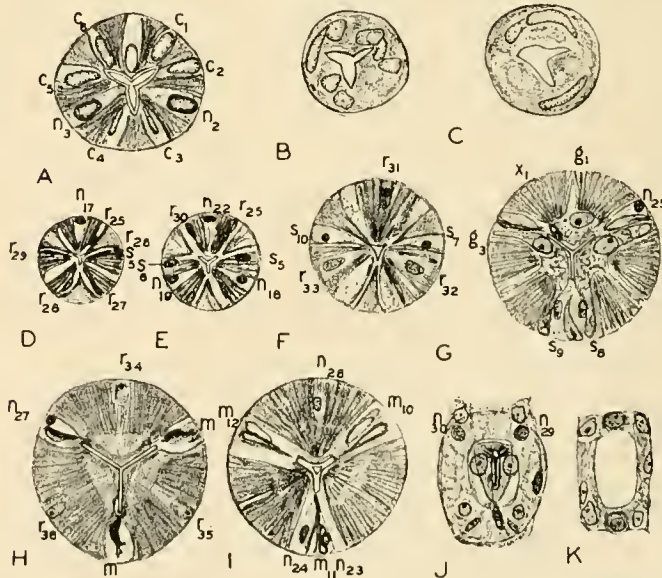


FIG. 86

esophago-intestinal valve). N-P—*Parucanthochus* sp. (N—Anterior part of corpus; O—corpus somewhat more posterior; P—esophago-intestinal valve).

FIG. 85. *Tripyllum carcinicolum* v. *eulkinsi*. (A—Stomatal region; B-C—corpus; D—bulbar region; E-F—esophago-intestinal valve).

FIG. 86. A-C—*Microloaimus* sp. (A—Corpus; B-C—esophago-intestinal valve). D-K—*Chromadora* sp. (D-I—Serial sections through bulbar region; J-K—esophago-intestinal valve).

All after Chitw. & Chitw., 1936, J. Wash. Acad. Sci., v, 26 (8).



ria) or the corpus may remain grossly distinct (*Axonolaimus*, *Aracolaimus*); the bulbar region is always rather elongate, never in the form of a definite bulb. As a rule one may distinguish procorpus and metacarpus in totomount specimens through the change in the esophageal lining (Fig. 15E) as the size of the marginal tubes becomes reduced; no forms are known with thickened attachment points for the radial muscles although the muscles themselves are concentrated.

The nuclei of the esophagus of axonolaimoids are essentially as in *Plectus* except that in some forms (*Sabatieria vulgaris*) the six posterior radial nuclei tend to assume a hexa- rather than a trisymmetry in their arrangement. The esophago-intestinal valve is as elongated as in plectoids and of slightly different form (Fig. 84 L-M); it contains about 10 to 12 nuclei.

Representatives of the superfamily Monhysteroidae are of three general types, linhomocoids, monhysterids and siphonolaims all characterized by a smaller number of radial nuclei than in plectoids and axonolaimoids. The Linhomocidae contains forms with a clavate esophagus which may (*Desmolaimus*) or may not (*Linhomocus*) be terminated by a well marked muscular swelling or bulb; the esophago-intestinal

valve is usually definitely elongated but may be rather short (*Sphaerolaimus*). In these forms the radial muscles are concentrated and this condition is usually accompanied by thickened cuticular attachment points on the lining (Figs. 82, 85, 87). The esophageal lumen while modified due to these attachment points is devoid of marginal tubes. Forms such as *Tripyllum carinicolum*, *Terschellingia pontica* and *Desmolaimus zeelandicus*, v. *americanus* have only 30 to 33 radial nuclei, the reduction or difference in number being in the metacarpus; the second group of marginals is also apparently lacking in *Terschellingia*. We find in these forms the same peculiar distribution of the radial nuclei of the posterior part of the bulb previously mentioned in the axonolaimoids (Fig. 90). The esophago-intestinal valve of linhomocoids is often associated with specially differentiated intestinal cells (*Tripyllum*) and

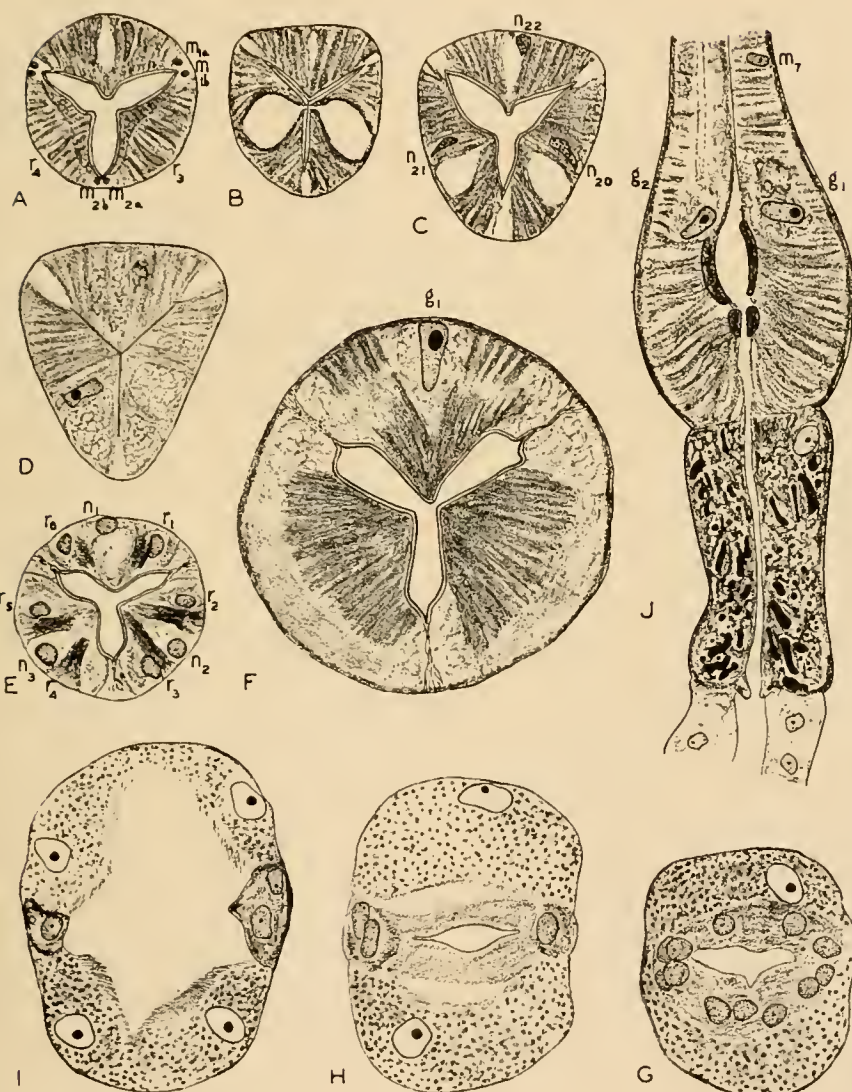


FIG. 87

FIG. 87. A-D—*Theristus setosus*. E-I—*Terschellingia pontica* (K—Corpus; F—bulbar region; G-I—serial sections through esophago-intestinal valve). J—*Desmolaimus zeelandicus* v. *americanus* (Longitudinal section through bulb, and esophago-intestinal valve).

FIG. 88. *Ethmolaimus revaliensis*. (A—Stomatal region; B—cor-

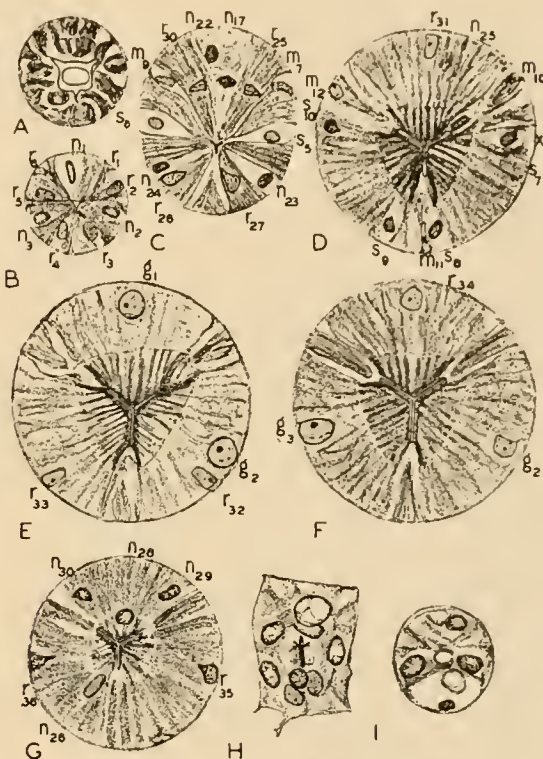


FIG. 88

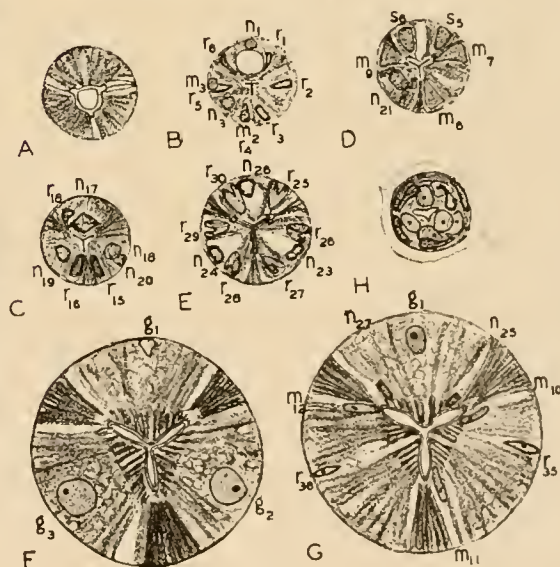


FIG. 89

pus; C-G—bulbar region; H-I—esophago-intestinal valve).

FIG. 89. *Monoposthia hexalata*. A-C—corpus (A—in stomatal region; B—just posterior to the orifice of dorsal gland; C—near base). D-G—bulbar region. H—esophago-intestinal valve.

All after Chitw. & Chitw., 1936, J. Wash. Acad. Sc., v. 26 (8).



in some forms such as *Desmolaimus* this structure forms a separate and distinct organ which may be termed the ventricular column (Figs. 82, 87J). Monhysterids (Figs. 82, 87A-D) have a more cylindrical esophagus, though never a distinct linhomoeid bulb, and the ventricular column is never elongated; the posterior radial nuclei have the same odd type of arrangement as linhomoeids but the radial musculature is of a dispersed type throughout, the esophageal lining without thickenings, the lumen very simply triradiate and the esophago-intestinal valve less elongate but otherwise similar to that of *Terschellingia* (Fig. 87G-I); the latter structure contains 19 to 23 nuclei. Siphonolaims have a very short corpus, an elongate isthmus, a short glandular bulbar region and a short esophago-intestinal valve containing six nuclei. The nuclei of the bulbar region are as in linhomoeids and monhysterids but only three marginal and 18 radial nuclei are present in *Siphonolaimus conicus*. Monhysteroids are peculiar in having very minute marginal nuclei (Fig. 87A).

In the suborder Monhysterina one first encounters paired pigment spots in the subdorsal or dorsolateral regions of the procorpus in a few genera of the Camacolaimidae (*Onchium ocellatum*) and Axonolaimidae (*Axocolaimus*). These peculiar structures are situated in the dorsal parts of the subventral sectors (dorsolaterally) or the lateral parts of the dorsal sector (subdorsally); there is, in the first mentioned genus, a pair of acorn like pigment masses each provided with a hyaline lens. While these are termed ocelli, no one has thus far connected them with sensory nerves. In *Monhystera paludicola* similar ocelli are situated in the body cavity dorsal to the esophagus.

CHROMADORINA.—In the suborder Chromadorina the esophago-intestinal valve is usually short though sometimes elongate but never dorso-ventrally flattened; it always retains its triradiate character. None of the representatives of this group preserve semblance to rhabditoid or plectoid esophagi.

In the Chromadoroidea the esophagus consists essentially of a cylindrical corpus and a bulbar region (Fig. 91); the esophageal lumen is triradiate, the lining unmodified, so far as known, though the radial muscles are definitely concentrated. Members of the Chromadoridae such as *Chromadora* and *Ethmolaimus revaliensis* have a very short esophago-intestinal valve containing 12 or 13 nuclei (Figs. 86, 88); 12 marginal and 36 radial nuclei are present in the esophagus, the posterior nuclei of the bulbar region being arranged in two typical groups of three. In *Microlaimus dentatum* the esophago-intestinal valve containing 11 nuclei is elongate reminding one of *Terschellingia*, but differs from that form in being triradiate (Fig. 86 B-C). Chromadoroids show no tendencies toward diminution in nuclear numbers such as was noted in monhysteroids but, rather the opposite. Several "additional nuclei" make their first appearance in this group; the arrangement and position of these nuclei (s, e, and x) are characteristic of both chromadoroids and desmodoroids (Fig. 90).

Cyatholaims generally have a much elongated tripartite bulbar region or a cylindrical esophagus. In representatives of the former type (*Paracanthochus coccus*) the lumen of the esophagus may be slightly enlarged marginally (Fig. 84 N-P). Choanolaims and tripyloids, on the contrary, have a typical triradiate lumen with long rays as in monhysterids rather than the short rays and minute lumen typical of the Chromadorina. All of these forms have a rather large and well developed but short esophago-intestinal valve.

Desmodoroids have the same general esophageal organization and the same general pattern of nuclear distribution (Fig. 89) as do chromadoroids but the esophageal lining may have thickened cuticular attachment points (*Metachromadora myrionides*).

The so called "multiple bulb" of chromadoroids and desmodoroids deserves special mention. In both superfamilies one may trace series of forms from a subspheroid bulb to a subcylindroid tripartite bulb thence to a cylindrical esophagus. The apparent sub-division of the bulbar region in forms such as *Monoposthia hexalata* and *Ethmolaimus revaliensis* (Fig. 91) into two parts is due to a particular arrangement of the musculature and glandular tissues and a break in the thickness of the esophageal lining at the points where one muscle ceases and another begins. This break indicates the separation of radial subgroups of muscles containing nuclei  $E_{21-23}$  and  $E_{24-26}$  respectively and is essential to the function of this type of bulb. The musculature containing the radial nuclei  $E_{27-36}$  is in the anterior part of the tripartite bulb and the corresponding muscles are a separate functional unit.

Pigment spots in the anterior part of the corpus are commonly found in members of the Chromadoridae and like those previously mentioned in the Camacolaimidae and Axonolaimi-

dae they are situated in the subdorsal marginal regions of the esophagus but in this case the pigment is diffuse rather than concentrated and is not provided with a lens. It seems proper to designate these as mere pigment spots while reserving the term ocelli for concentrated pigment bodies accompanied by lenses. De Man (1889) described true ocelli situated dorsal to the esophagus in the body cavity of *Cyatholaimus demani* (Syn. *Cyatholaimus ocellatus* of de Man).

The esophagi of desmoseoleoids have not as yet been adequately studied. The esophagus is grossly rather cylindroid but narrow, the three esophageal glands projecting posteriorly indicating a reduction in the musculature of the bulbar region. Such forms (Fig. 17) have well developed, brilliantly colored pigment bodies dorsal to the base of the esophagus.

ENOPLIDA.—The esophagi of representatives of this order commonly (always?) have five or more uninucleate or multinucleate esophageal glands. The esophagus usually has an elongate muscular anterior part followed by an elongate glandular posterior part, such divisions resembling those of spiruroids and filarioids. The location of the esophageal gland orifices varies widely in the group.

ENOPLINA.—Esophagi of representatives of this sub-order have been studied by Marion (1870), de Man (1886, 1904), Jägerskiöld (1901), Türk (1903), Rauther (1907) and the writers (1937). In general we find two types of esophagi in this group: the first type in which the esophageal glands have orifices rather near their nuclei, that is, in the posterior glandular part of the esophagus (such forms are included in the superfamily Tripyloidea); and the second type, in which the subventral esophageal glands open anteriorly either near the base of the stomatal region or in subventral teeth (such forms may occur in either of the superfamilies Enoploidea or Tripyloidea).

In the Tripyloidea the esophagus either is cylindrical (*Prionchulus*, *Tripyla*) or consists of an elongated narrow corpus and a slightly wider elongate glandular region (*Alaimus*); in all such forms studied there are five uninucleate esophageal glands, one dorsal and four subventral (Fig. 91). Mononchs such as *Prionchulus muscorum* have concentrated radial muscles and well developed cuticular attachment points (Fig. 92); the esophago-intestinal valve which is triradiate and quite massive (Fig. 92M), contains 22 nuclei in *P. muscorum*. A total of 36 radial and nine marginal nuclei have been observed, the radials (12 in procorpus, 12 in metacarpus and 12 in glandular region) are arranged in sets of six, indicating that even those of the posterior group act as a single unit rather than as two units as in rhabditids, plectids and chromadorids. Nuclear distribution (Fig. 90) indicates quite definitely that the glandular region of the esophagus of *Prionchulus* as well as other tripyloids, enoploids and dorylaimoids is homologous to the bulbar region of the orders Rhabditida and Chromadorida rather than the glandular region of spiruroids since it does not contain the radial nuclei characteristic of the metacarpus (total number of radials 18 in spiruroids). The five esophageal gland nuclei are subequal in size and each of the accompanying glands opens nearly directly into the esophageal lumen (Fig. 94D).

In *Tripyla papillata* and *Trilobus longus* the musculature is dispersed, no cuticular attachments are present and the esophago-intestinal valve is quite massive, consisting of an external part containing six or seven large nuclei and an internal part containing up to 100 nuclei (Fig. 94 E-L). This peculiar structure, sometimes termed a pseudo-bulb, or bulb, is commonly thought to be a part of the esophagus proper but this does not appear to be the case. It is a further development of the type of valve found in *Prionchulus*. The five esophageal glands are similar to those of the latter genus except that the dorsal and the first pair of subventral esophageal glands extend to the base of the stomatal region where they open.\* *Alaimus* is similar to *Tripyla* except that the radial muscles are concentrated; the triradiate esophago-intestinal valve is quite small and inconspicuous, and the subventral glands do not extend beyond the enlarged glandular region.

In the superfamily Enoploidea the gross form of the esophagus varies considerably, there being types with a cylindrical esophagus, types in which the narrow corpus is followed by a gradually expanding elongate glandular region (conoid) and types in which the corpus is slightly narrower and set off internally from an elongate cylindrical bulbar region. Due to

\*On the basis of esophageal structure the current concept of the superfamily Tripyloidea must be revised, preferably to include the Ironidae. The position of the gland orifices as previously stated for *Tripyla* (pp. 16 and 52) is not in accordance with present findings. Temporarily, the absence of cuticular duplication at the head may be considered the limiting character of the Tripyloidea (including the Ironidae) as opposed to the presence of cuticular duplication in the Enoploidea. Later we hope to be in a position to add further characters to substantiate this revision.





FIG. 90

Tables of esophageal nuclear distribution of Aphasmodians. Chitw. & Chitw., 1936, J. Wash. Acad. Sc., v. 26 (8) & 1937, v. 27 (12).

the distribution of radial muscles the conoid type of esophagus may be multibulbar (*Polygastrophora*, *Bolbella*), crenate in outline (*Phanodermopsis*) or smooth in contour (*Oxystomina*, *Eurystomina*, *Leptosomatum*). Among the latter, two types are distinguishable in regard to the muscular development. In *Oxystomina* and its relatives the musculature is poorly developed while in the remaining forms it is well developed.

In the Oncholaiminae the esophagus is of a cylindrical type, the esophageal lining simple, the lumen also simple and tri-radiate throughout; the esophago-intestinal valve is triradiate, moderately elongate and contains numerous nuclei. There are 12 marginal nuclei but only 27 radial nuclei in *Metoncholaimus*

*pristinus* and according to their distribution (Fig. 90), we may judge that compared with *Tripylla*, the third group of radial nuclei (of *Metoncholaimus*) represents a case of failure of cleavage of the last set of radials of the corpus of *Tripylla*. In the latter form the final cleavage results in the third and fourth sets (RIII and RIV) or 12 nuclei while in *Metoncholaimus* only six nuclei are present. Likewise the three giant radial nuclei (Fig. 94 O P) of the bulbar region also may represent a cleavage failure. In this form one dorsal and two pairs of subventral gland nuclei are to be found in the posterior part of the esophagus; separate orifices of the two glands in each sector have not been distinguished. The

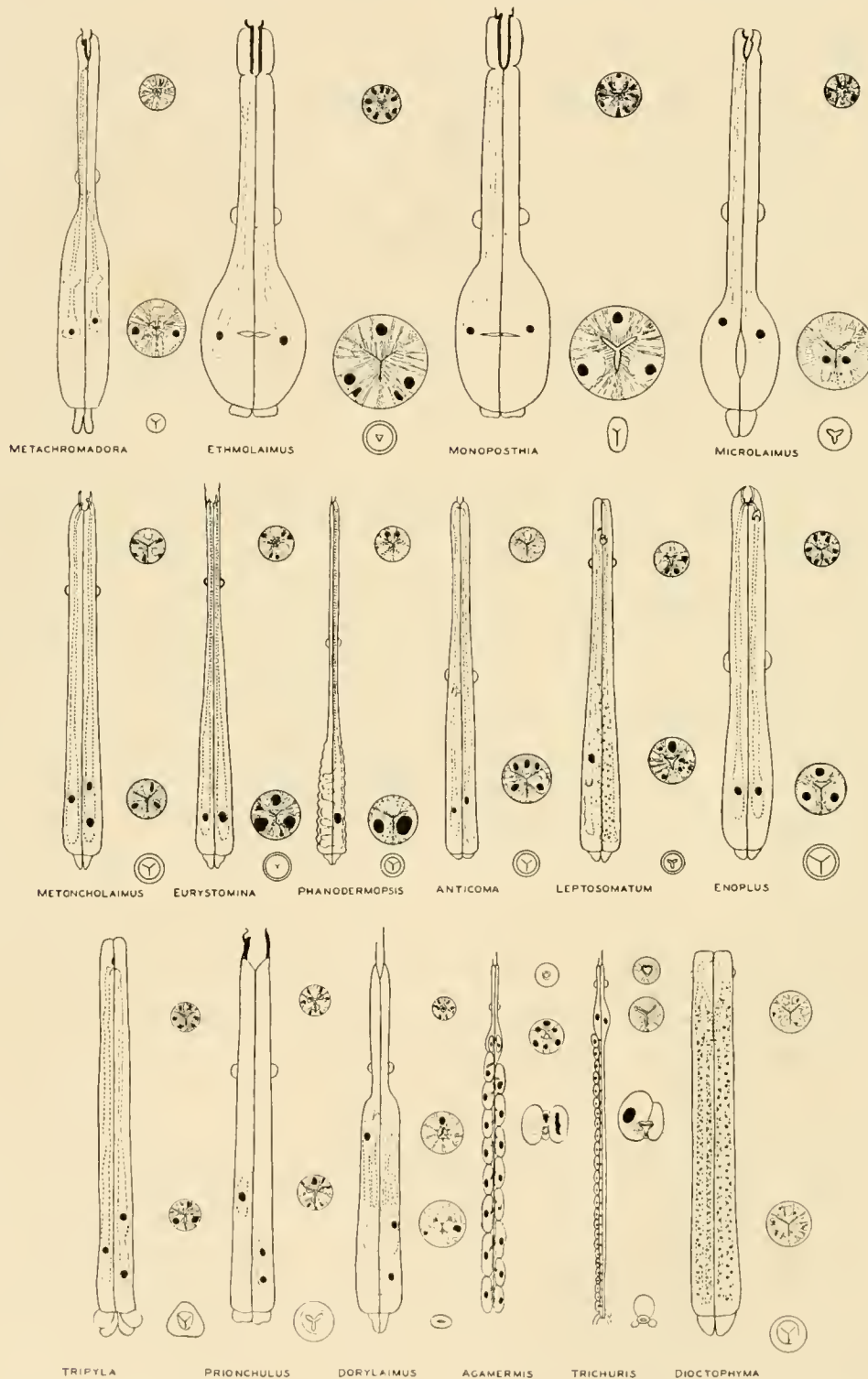


FIG. 91

Diagrams of esophagi including representatives of the Desmodoroidea (*Metachromadora*, *Monoposthia*), Chromadoroidea (*Ethmolaimus*, *Microlaimus*), Eno-

ploidea (*Metoncholaimus* to *Enoplus*), Tripyloidea (*Tripylla*, *Prionchulus*), Dorylaimoidea, Trichuroidea and Dioctophymatoidea. Original.



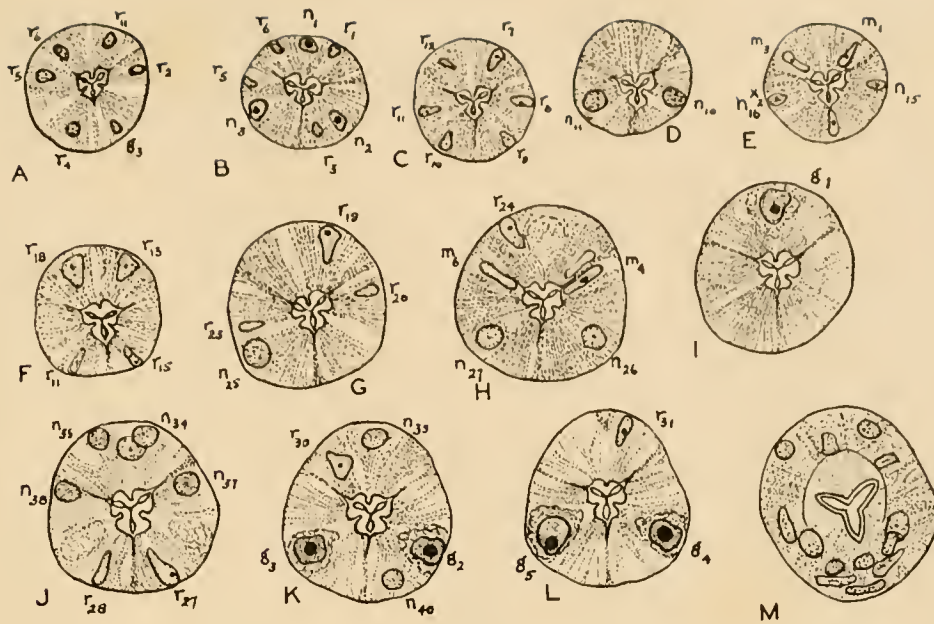


FIG. 92

*Prionchulus muscorum*, sections (a few left out) in series, M—esophago-intestinal valve. Original.

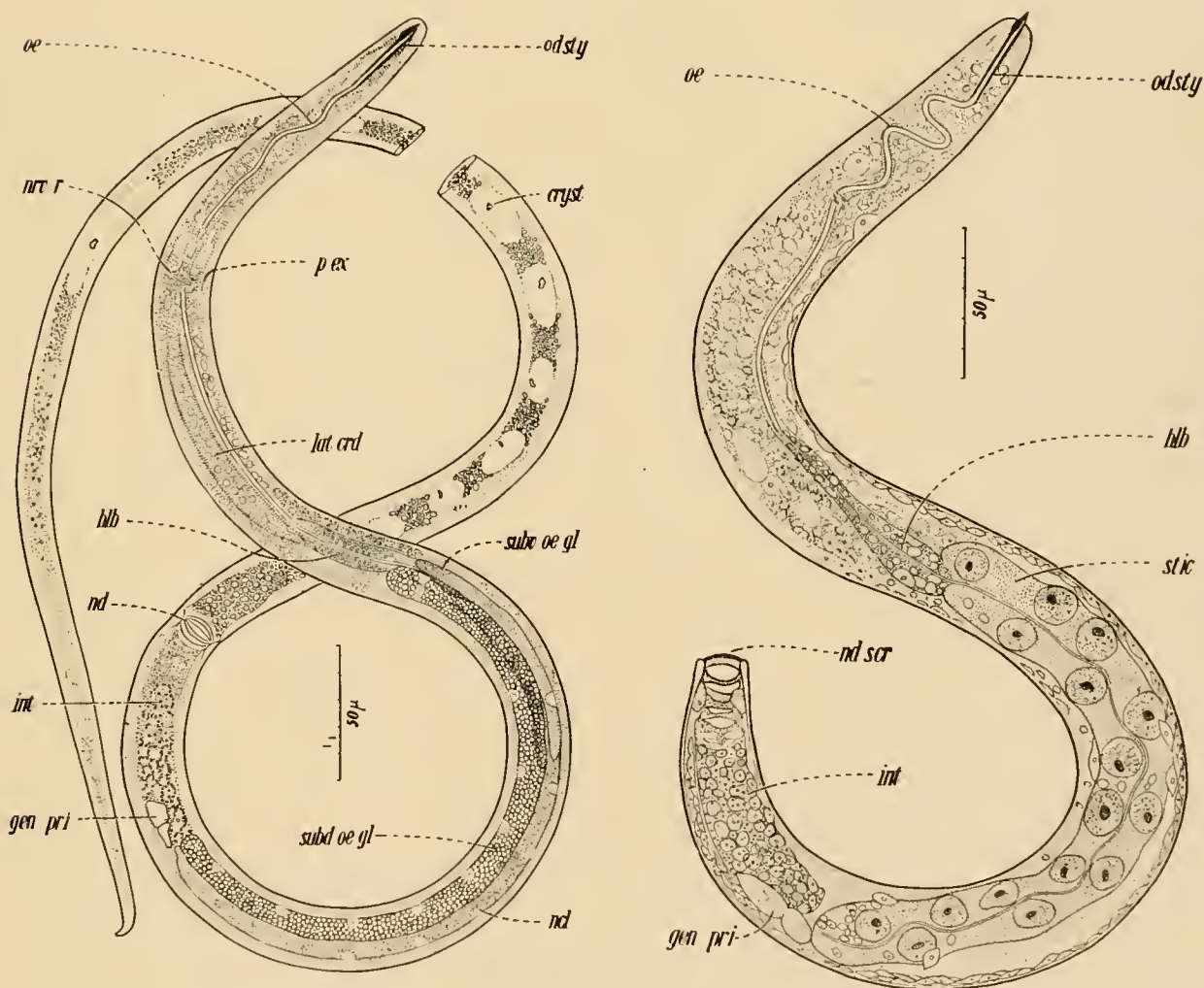


FIG. 93

*Agamermis decoudata*. A—Preparasitic larva. (Note primary esophageal glands, subd. oe. gl., subv. oe. gl.). B—Larva after 4 days in

host. (Note development of stichocytes.) After Christie, 1936, J. Agric. Res., v 52 (3).



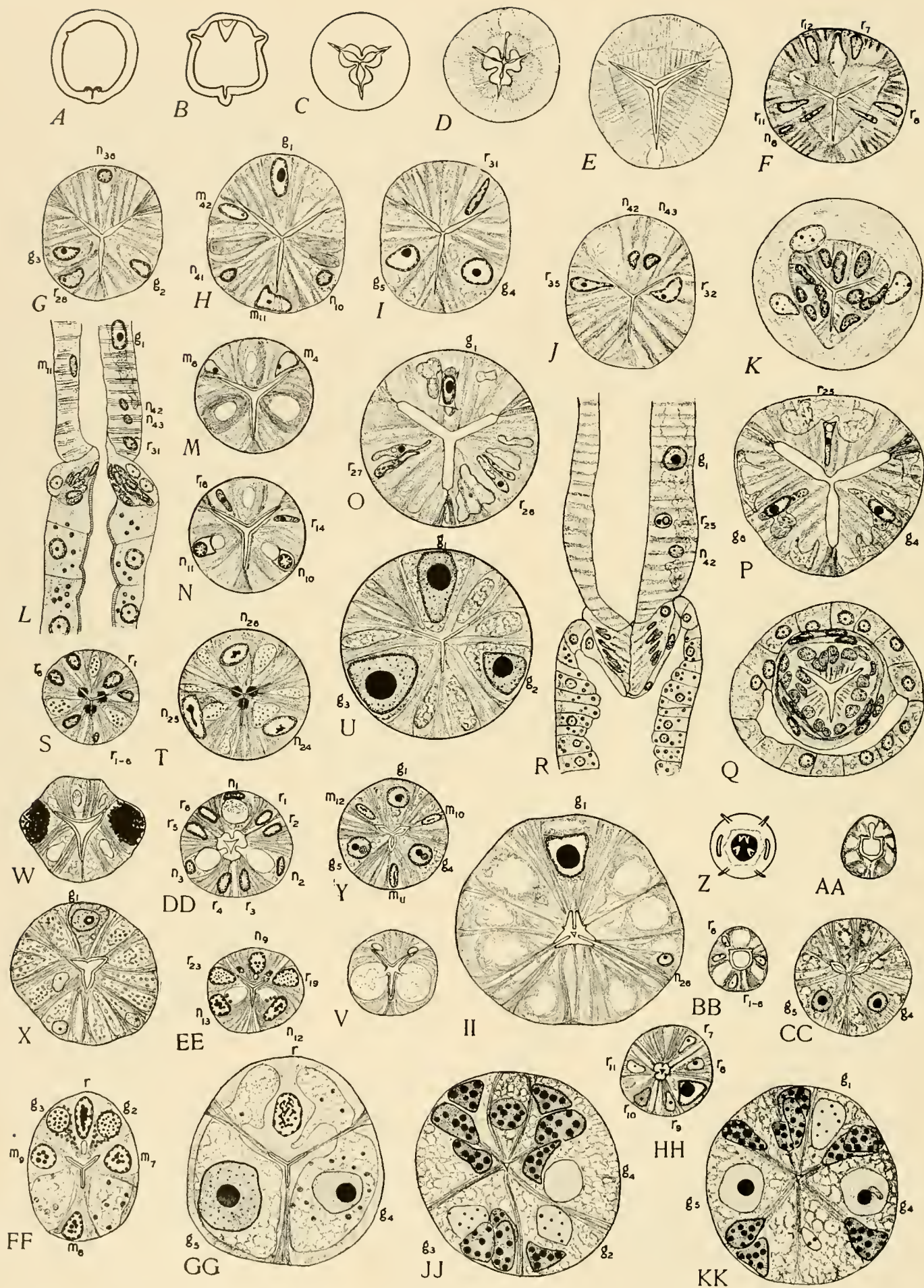


FIG. 94  
 Esophagi of members of the Enoplida. A-D—*Prionchulus muscorum* (A-B—Showing cuticular lining in the stomatal region; C—procarpus; D—bulbar region at level of dorsal gland orifice) E-L—*Tripyla papillata*. (E—Stomatal region; F—corpus; G-I—Bulbar region (glandular); K—esophago-intestinal valve or "pseudobulb"; L—Longitudinal through regions covered by H-K). M-R—*Metoncholaimus pristurus*



glandular protoplasm of the subventral sectors seems to be continuous and one concludes that in this case the subventral glands are binucleate; the ducts from all three glands extend anteriorly into the teeth of the stoma where each opens in a minute pore. Rauther (1907) recorded four esophageal glands in the subventral sectors of *Oncholaimus vulgaris*. He found separate pores for the hindmost pair situated somewhat anterior to the nerve ring and dorsal to the center of their respective sectors.

*Eurystomina americana* has a very similar esophagus to *Metoncholaimus* but its narrow part (corpus) has distinct cuticular attachment points and the musculature is concentrated in the corpus (Fig. 94T) but not in the bulbar region; 30 radial nuclei are present, there being 18 in the corpus as in *Metoncholaimus*, but there are 12 in the glandular (bulbar) region arranged in two sets of six as in *Tripyla* and *Prionchulus*. The esophageal glands extend the entire length of the esophagus as in oncholaims but only three gigantic gland nuclei (Fig. 94U) have been observed, the right subventral being much the largest. Only eight nuclei have been seen in the esophago-intestinal valve, the anterior part of which is triradiate while the posterior part is dorsoventrally flattened.

*Enoplus communis* has a cylindrical esophagus more like that of oncholaims than *Eurystomina* but 33 radial nuclei are present, the corpus containing the full number of 24 nuclei as in *Tripyla*, while the bulbar region (glandular part) contains only nine as in *Metoncholaimus*, the last group of three indicating again a case of suppressed cleavage (Fig. 95A-AA). There are three large subequal esophageal gland nuclei in the bulbar region and the corresponding glands each has an orifice at the anterior end of the esophagus, at the base of the teeth. The short, well developed, triradiate esophago-intestinal valve of *Enoplus* contains 11-15 nuclei (number questionable). Rauther (1907) obtained the same total as the writer's (i.e., 109 nuclei which includes nerve cell nuclei and esophago-intestinal valve nuclei) but he differs in some cases as to the functions he attributes to specific ones. He also describes two lateral glands (the nuclei of which we designate  $x_{1-2}$  in Fig. 90 & 95S) near the mid region of the esophagus which open anteriorly near the level of the amphids in the marginal region. We agree that these probably are esophageal glands but were unable to distinguish their orifices.

The esophagus of *Phanodermopsis longisetae* is interesting because it is representative of forms with a crenate glandular esophagus which is commonly termed "cellular." The illusion of cells (Fig. 91) is created through the localization of extremely sparse musculature at intervals, separating swollen regions of nearly exclusive glandular tissue. Though the esophagus is conoid and crenate the nuclear distribution is similar to that found in *Enoplus* with the following exceptions: There are 36 radial nuclei, the most posterior group being subdivided into two sets of three nuclei; the two chief subventral gland nuclei are much enlarged as are the glands, while the dorsal gland nucleus is situated far forward and much reduced in size, and the small subsidiary (lateral glands of Rauther) subventral gland nuclei are situated near the dorsal gland nucleus (Fig. 94FF). The chief subventral glands (Fig. 94GG) empty into the stoma while the dorsal and subsidiary glands appear to have their orifices posterior to the nerve ring.

*Leptosomatium elongatum*, representative of still another type, has multinucleate subventral esophageal glands. The conoid esophagus is of smooth contour, somewhat vesiculate internally. The anterior part (corpus) contains the same nuclei found in *Phanodermopsis* while the posterior part contains such a large number of nuclei (about 23 in each chief subventral gland) that it would be difficult to designate the types accurately. The dorsal gland is uninucleate, the nucleus (Fig. 94X) much larger than other nuclei of the esophagus; the subventral gland orifices are at the anterior end of the esophagus while the dorsal gland orifice is somewhat further

posterior. In the corpus the musculature is concentrated (Fig. 94W) and the esophageal lining thick but without attachment points. According to Jägerskiöld (1901), Turk (1903) and Rauther (1907) the esophagi of the related genera *Thoracostoma* and *Cylicolaimus* (which are grossly cylindrical) have similar esophagi except that the esophageal lining has definite cuticular attachment points. Rauther was able to distinguish small subsidiary subventral (lateral) glands as in *Enoplus*. Other enopliids, such as *Anticoma* (Fig. 94V) and *Rhabdodemania*, with cylindrical esophagi have gland orifices in similar positions to those above described, with a simple i.e., enoplioid esophageal lining.

In the whole order Enopliida pigment spots or ocelli occur only in the superfamily Enoploidea, families Enopliidae and Oncholaimidae, and are of sporadic appearance in these groups. In the Oncholaiminae such pigment is rather diffuse in the musculature of the corpus while in *Enoplus* it is concentrated in a pair of subdorsal spots in the marginal areas near the anterior end. Well developed "ocelli" have been described in Leptosomatids, phanodermatids and enchelidiids.

Finally we come to the family Ironidae which in many ways appears to have closer affinities with the Mononchidae and Dorylaimidae than with other enopliids. *Ironus* (Fig. 94Z-CC) and *Ironella* have cylindrical esophagi with well developed cuticular attachment points, concentrated radial muscles, and 5 subequal esophageal glands. Like *Enoplus*, *Oncholaimus*, and *Tripyla*, three of the glands have orifices into the stomatal region. *Cryptonchus nudus*, though otherwise very similar to *Ironus*, has its esophageal glands confined to the posterior part of the esophagus (Fig. 94DD & Y). It seems, therefore, to be intermediate between such forms as *Prionchulus* and *Ironus*.

**DORYLAIMINA.**—This suborder is perhaps more compact in fundamental esophageal organization than the suborder Enopliina though the gross morphology is certainly more diverse and includes more odd types (Fig. 91). Dorylaimins have one point in common with each other and with the family Mononchidae, namely that none of the esophageal glands extend to the stomatal region. The suborder contains superfamilies with esophagi of two types, one in which the glandular region is tremendously elongated, the subventral glands reduplicated and protruding from the esophageal contour, and the other in which the glandular region is either short or only moderately elongated, and in which only two pairs of subventral glands are present. This latter group includes the soil and aquatic species of the superfamily Dorylaimoidea while the former group includes the parasitic nemas of the superfamilies Mermithoidea and Trichuroidea.

Dorylaimoids have a cylindrical corpus followed by either an elongated cylindrical glandular region (Dorylaimidae) or a short pyriform glandular region (Diphtherophoridae, Leptotrichidae) the parts sometimes separated in the latter instance by a more or less distinct isthmus; the esophageal lumen is subtriangular anteriorly, rapidly becoming minute and triradiate with marked cuticular thickenings of the esophageal lining (Fig. 94HH); the musculature is strongly concentrated. The radial musculature is well developed throughout the esophagus in leptotrichids and dorylaimids but rather degenerate in the glandular region of diphtherophorids.

*Dorylaimus obtusicaudatus* has an esophagus extremely similar to that found in *Prionchulus* for the anterior part (corpus) contains four sets of six radial nuclei (three sets in the narrow part, one at the junction of the anterior and posterior parts) and only one set of three marginals (Fig. 90); the posterior glandular (bulbar) region contains two sets of six radial and two sets of three marginal nuclei, the hindmost set of radials being somewhat subdivided but arranged in a manner indicating they act as a unit. Each of the five esophageal glands has its orifice near the level of the nucleus with a very short duct. The dorsal gland bifurcates, each branch continuing to divide dichotomously and the branches enter the subventral sectors, eventually coming to fill the entire non-muscular part of the esophagus anterior to the subventral glands (Fig. 94II). These latter are found in two pairs considerably posterior to the dorsal gland; the first subventral gland on the right side is considerably smaller than the others. The esophago-intestinal valve of dorylaimids is very well developed, elongate, dorsoventrally flattened, and contains 27 nuclei.

There is in addition to the usual number of nuclei of the esophagus a large nucleus in the left subventral sector which, with its surrounding protoplasm, acts as a generative nucleus of the stylet (Fig. 94III). As previously stated the stylet is formed in the procorpus and moves anteriorly to take its final position attached to the anterior end of the esophageal lining.

*Leptonchus* has an esophagus apparently identical internally

(M-N—Corpus; O-P—bulbar region; Q—esophago-intestinal valve; R—longitudinal sagittal through regions shown in O-Q dorsal to reader's right). S-U—*Eurystomina americana* (S—anterior part of corpus; T—posterior part of corpus; U—glandular region). V—*Anticoma litorea*. Near anterior end of esophagus, subventral gland orifice and subdorsal (dorsolateral) ducts. W-X—*Leptosomatium elongatum* v. *acephalum*. (W—Region of ocelli, 5 ducts also visible; X—glandular region). Y-JI—*Cryptonchus nudus*. (Y—posterior end of glandular region; JI—corpus). Z-CC—*Ironus ignavus* (Z—head; AA—dorsal gland orifice; (stomatal region); BB—beginning of corpus or end of stomatal region; CC—posterior part of glandular region (corpus proper is like fig. DD). EE-GG—*Phanodermopsis longisetae*. (EE—Posterior part of corpus; FF—anterior part of glandular region; GG—posterior part of glandular region). HII-II—*Dorylaimus obtusicaudatus*. (HII—Corpus at level of stylet cell; II—glandular region at level of dorsal gland nucleus). JJ-KK—*Triplonchium* sp. (Glandular region showing five esophageal gland nuclei.)



with that of dorylaimids but only three large esophageal glands have been observed; presumably both of the first pair of subventral glands in this instance are small. *Triplonchium* of the Diphtherophoridae has very feebly developed, if any, thickened cuticular attachment points of the esophageal lining, and the dorsal and first pair of subventral gland nuclei (situated at the same level) is only slightly smaller than the posterior subventral pair (Fig. 94 JJ-KK).

The esophagi of the mermithoids have been studied by Rauter (1906), Hagmeier (1912), G. W. Müller (1931), Christie (1936) and the writers (1935, 1937) as well as many others who have added scattered bits of information. The peculiarity of the mermithoid esophagus is its relatively great length and tenuousness. In the adult stage, which does not feed, the greater part of the esophagus posterior to the nerve ring appears as a slender tube covered with a bit of protoplasm to which various types of cells are attached at intervals. The esophageal musculature appears to be entirely degenerate. One must turn to the larval stages of mermithids for an understanding of these structures.

The preparasitic larva has an esophagus consisting of a short anterior part terminated by a muscular swelling and followed by an elongate narrow posterior part with which glands are associated. There are three unicellular elongate esophageal glands extending posteriorly into the body cavity from the base of the anterior (non-glandular) portion, the dorsal being considerably larger than the subventrals; these *primary glands* (Fig. 93) become atrophied after the entrance of the larva into its host. In addition there is a double series of large cells (stichocytes) attached to and co-extensive with the posterior part of the esophagus. These cells are secondary esophageal glands, probably representing a reduplication of the posterior pair of subventral esophageal glands of dorylaims and enoplids. In the parasitic stage these glands become much enlarged (Fig. 93) and later they too atrophy as the larva approaches adulthood. The lining of the esophagus of mermithids is rather clearly triradiate in the preparasitic larva, becoming subtriangular in later stages until finally the basic triradiate character is scarcely discernible (Fig. 96A-E). In *Agamermis decaudata* 48 large nuclei corresponding to the marginals and radials are present, most of them arranged with little indication of pattern, and there is even less indication of muscular fibers in the parasitic larvae (Fig. 96). There are 27 such nuclei anterior to the orifices of the primary glands indicating that this region corresponds to the corpus while there are 21 in the posterior part, indicating that it corresponds approximately to the bulbar region. These nuclei are situated within the wall of the esophagus proper. Each of the glands of both types has an orifice not distant from its nucleus. There is one peculiarity of the esophagus which does not seem reconciled with the tremendous esophageal gland development in the parasitic stage, namely, that the lining disappears posterior to the orifice of the last stichocyte and the lumen does not connect with the degenerate intestine. The stichocytes are quite obviously functional and it is difficult to believe that fluid food is not drawn in through the esophagus but if so, we do not know its destination. The number of stichocytes varies from four to 16 or possibly more, according to the particular form.

The peculiar esophagus of trichuroids has long been a subject for study. Eberth (1860, 1863), Leuckart (1866), Rauter (1918), G. W. Müller (1929), Christenson (1935) and the writers (1929, 1935, 1937) have investigated various forms of this group. Ward (1917) proposed a separate suborder for trichuroids and mermithoids (Trichosyringata) based on the peculiarity of the esophagus. The esophagi of mermithoids and trichuroids are similar but not fundamentally different from other nematodes. Ward stated "A type of radically different character is the capillary esophagus . . . It consists of a row of cells, pierced throughout its entire length by a delicate tube." The cells of which he speaks are stichocytes or esophageal glands attached to but not "pierced by" the esophagus proper which is to a greater or lesser degree embedded in these cells. As in mermithids, the wall of the esophagus contains its own nuclei. Much discussion has centered around the significance and nature of the structures, but since the points now are clear, further discussion seems unnecessary.

The anterior part of the esophagus of *Trichuris oris* is narrow and muscular, terminated by an elongated swelling; the lumen is triradiate, the lining thick but without attachment points. Within this region, besides nerve cells, one group of three marginal nuclei and two groups of six distinct radial nuclei are present. On this basis one might presume it to be the procorpus but within the terminal swelling a set of three

large nuclei of esophageal glands is present (Fig. 91 & 96I). These glands, whose orifices are posterior to the nerve ring, doubtless correspond to the primary glands of mermithids. The posterior part of the esophagus is quite narrow and embedded in a single series of large cells (cell body "zellkörper" of authors). The narrow "tube" or esophagus proper is triradiate to hexaradiate and has its own wall containing radial nuclei as well as nerve cells occurring at intervals. Contrary to general supposition, this wall contains well developed radial muscle fibers (Fig. 96M). The large cells in which it is embedded are esophageal glands, each having a separate orifice reached or formed by a tube through the esophageal wall. This being the case, there is no fundamental difference from other nematodes in which the esophageal glands may come to lie outside the esophageal contour (*Contracaecum*, *Aphelenchus*, *Onchium*). Because of the fact that in larval trichuroids the stichocytes are more or less alternately paired and the orifices in the adult tend to alternate it seems reasonable to assume that the single row stichosome of *Trichuris* is a later evolutionary development from a double row of stichocytes such as is found in mermithoids. This view is supported by the illustrations of Janieki and Rosin (1930) of the esophageal region of *Cystoopsis* which shows two rows of stichocytes. The number of stichocytes seems to be variable to some extent within a given species of trichuroid.

At the end of the esophagus, unlike mermithoids, we find a direct connection of the esophagus with the functional intestine formed by a dorsoventrally flattened esophago-intestinal valve such as is present in dorylaimoids. Two large cells (Fig. 96O) described as glands with direct openings into the esophageal lumen, by Eberth (1860, 1863), are attached to the esophagus at its base. Neither Rauter (1918) nor the writers were able to distinguish any protoplasmic connection of these cells with the esophageal lining or any tubules in the cytoplasm of these cells. It now seems possible that these cells are enlarged mesenterial cells, homologous to the series of smaller cells supporting and covering the esophagus and stichosome (p. 45).

**DIOCTOPHYMATINA.**—The esophagus of the suborder Dioctophymatina has received little attention since the first report of Schneider (1866) that the walls of the cylindrical esophagus of such forms contain numerous longitudinal "tubes." No additional information was added until the subject was recently reopened by the writers (1937). The esophageal lining is simple, the lumen triradiate and the well developed musculature dispersed in representatives of this group. There is no division, either grossly or internally, into anterior and posterior parts. The three massive esophageal glands have their orifices at the anterior end of the esophagus and begin branching dichotomously near the level of the nerve ring; glandular tissue is thereafter interspersed between the radial fibers to the base of the esophagus. It appears that there are 36 radial and nine marginal (or possibly 12) nuclei in the esophagus. The radials are arranged in subgroups of three, one near the center of each sector. The esophago-intestinal valve is triradiate.

The highly remarkable esophageal glands deserve special note. Each has a short *terminal duct* lined with cuticle, followed by a short, thick walled *primary tubule* which bifurcates into secondary tubules. In *Soboliphyme baturini* the secondary tubules appear to be lined with cilia (Fig. 95FF). Here and in *Eustrongylides* these secondary tubules branch dichotomously, time after time, throughout the length of the esophagus and come to nearly fill the non-muscular part of their sectors (Fig. 95CC-DD) but do not enter other sectors. The marginal tubules end blindly (Fig. 97C) and their position is taken by others formed by the branching of the more centrally located tubules. In *Dioctophyma renale* the same condition exists with the exception that the secondary tubules of the dorsal gland do not undergo further branching (Fig. 95BB) and tubules from the subventral glands take a marginal position in the dorsal sector (Fig. 97B). In all cases we find dense glandular protoplasm containing numerous gland nuclei (Fig. 95CC-DD) surrounding the tubules. There are literally hundreds of such nuclei. Whether the subventral glands correspond only to the anterior pair of subventral esophageal glands or to both anterior and posterior pairs of subventral glands of enoplids is uncertain.

The dioctophymatid esophagus resembles the enoplid esophagus in the position of the orifices of the esophageal glands and also resembles to some extent that of the leptosomatids in the multinucleate condition of the glands. However, the peculiar dichotomous branching of the tubules has its only parallel in the branched dorsal gland of *Dorylaimus*.



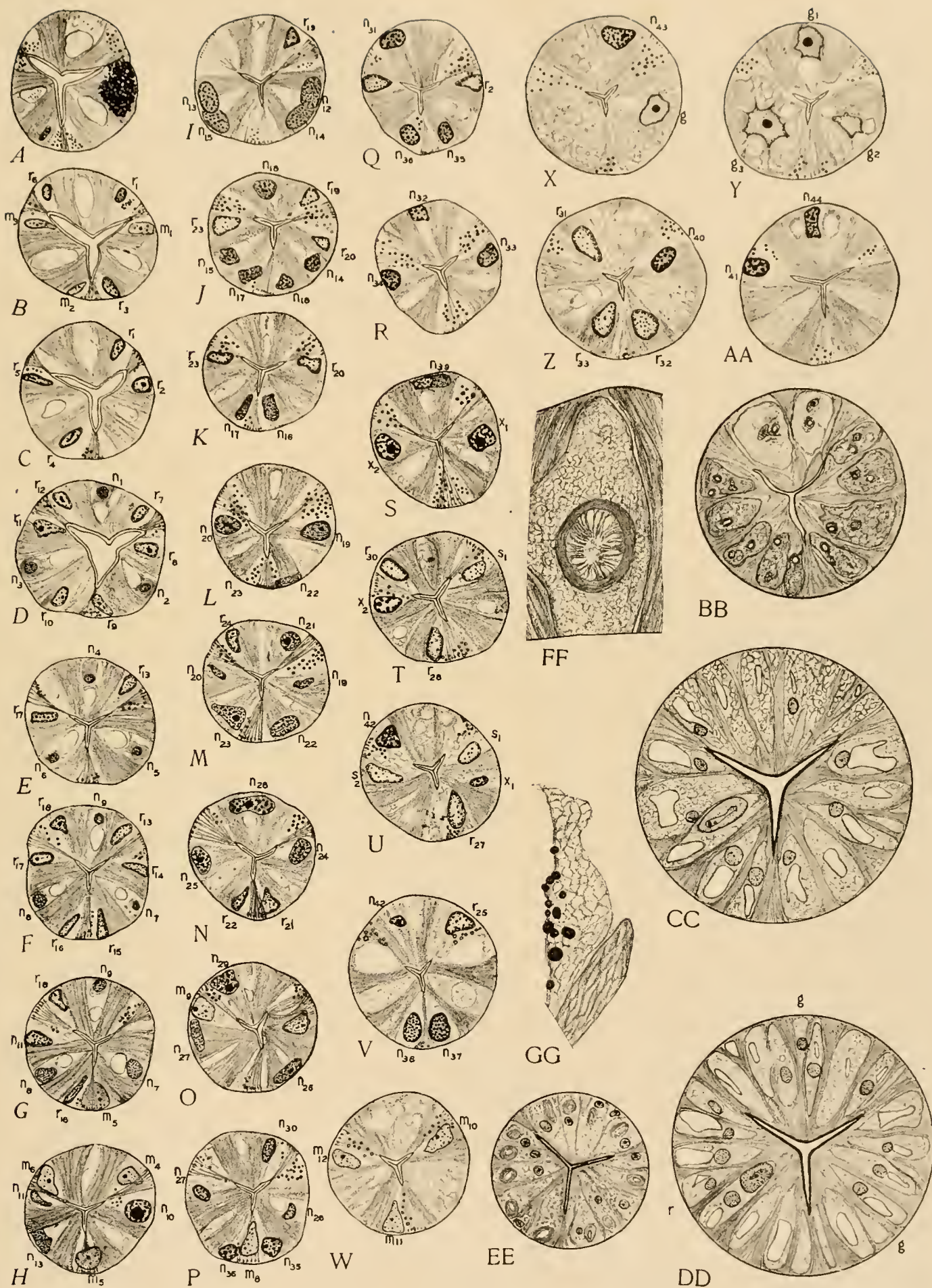


FIG. 95  
A-AA—*Enoplus communis* v. *meridionalis*. (Serial sections with a few left out.) BB—*Diactophyma renale*. CC-GG—*Soboliphyme baturini*. (CC—basal region of esophagus, radial nucleus also showing); DD—



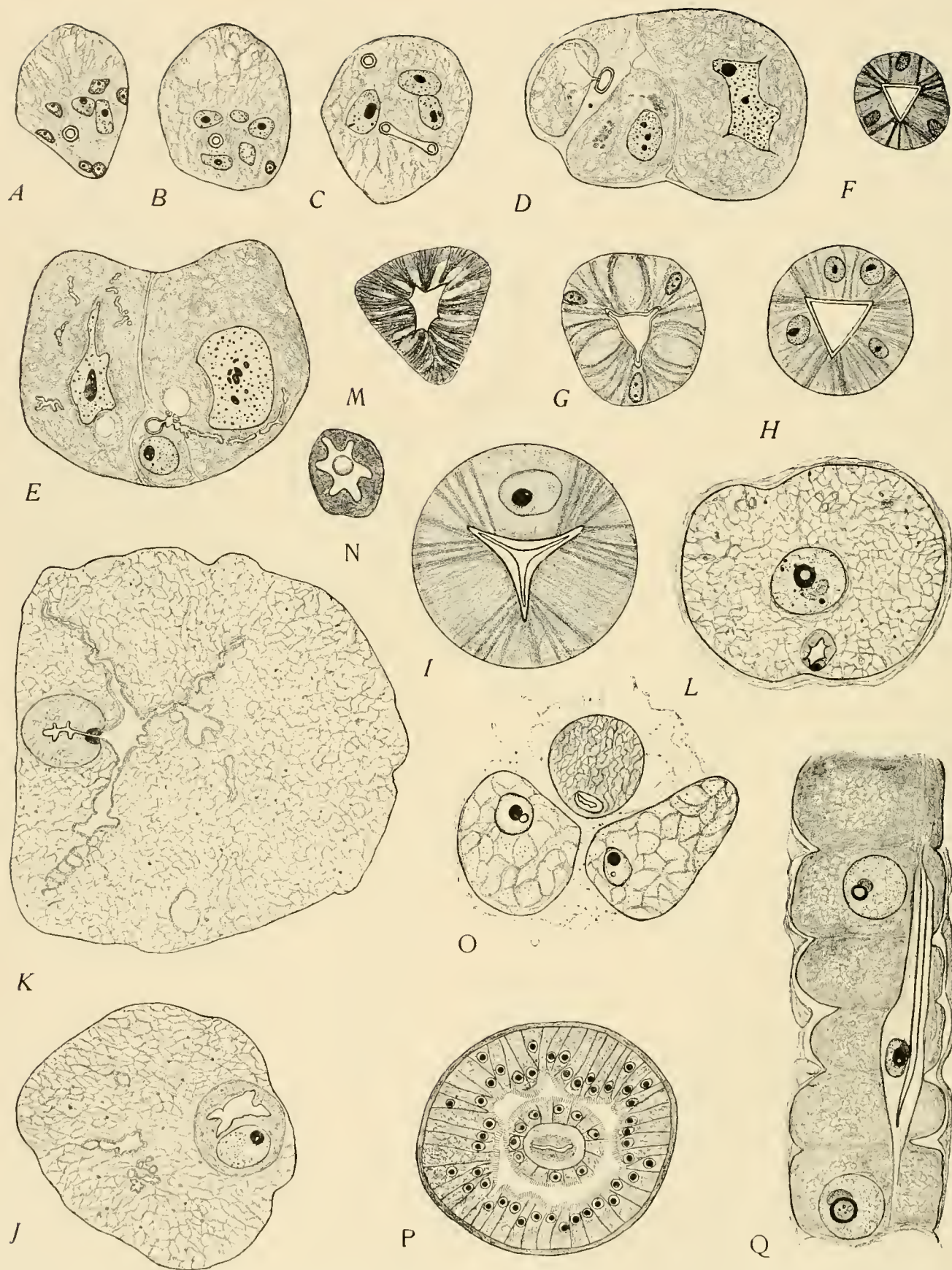


FIG. 96. A-E—*Agaveermis decandata*. (4 mm long parasitic larva.) (A-B—Anterior end of esophagus containing problematic nuclei, small, and first group of radial nuclei, larger; C—just anterior to nerve ring including  $r_{n-12}$ ; D—at posterior level of primary glands showing most posterior gland orifice and one primary gland nucleus, the other gland stopped anterior to this section. Large cell to the right is the first stichocyte; E—mid-stichosome region showing esophageal tube, r type nucleus, two stichocytes and branched tubule). F-Q—*Trichuris ovis*. (F—Section through 3 anteriormost nuclei  $s_{1-3}$ ; G—section at level of first marginal group; H—section at level of first radial group; I—

FIG. 96

section dorsal primary esophageal gland. J—stichocyte enclosing esophagus at level of radial nucleus; K—tubule orifice and branching; L—stichocyte surrounding esophagus in wall of which there is a small nucleus (? nerve); M—esophageal wall from stichosome surrounded region, stained with fuchsin to show musculature; N—Esophageal wall from stichosome surrounded region containing red blood corpuscle in lumen; O—End of esophagus with 2 accompanying cells (lower); P—Esophago-intestinal valve and intestine; Q—Longitudinal section showing relationship of stichocytes and radial muscle cells to esophageal lumen). Original.



## 2. ESOPHAGO-SYMPATHETIC NERVOUS SYSTEM

The presence of nerve cells in the wall of the esophagus was first mentioned by Looss (1896) and this system was described briefly in *Ancylostoma duodenale* by that writer in 1905. Later (1910) Goldschmidt studied the system in *Ascaris lumbricoides* followed by Martini (1916) in *Oxyuris equi*, Linnick (1921, 1924) in *Strongylus edentatus*, de Bruyn (1934) in *Angusticaecum holopteron*, and various observations by the writers (1933, 1937) refer to free-living and parasitic forms.

In substance, this system consists of three longitudinal nerves, one situated near the center of each sector and extending from the base nearly to the anterior end of the esophagus (Fig. 97R). These nerves contain in their course a series of nerve cells and two or three commissures joining the longitudinal nerves. In most forms we find a commissure at the base of the corpus, another in the anterior part of the bulbar region and a third in the posterior part of the bulbar region. Nerve cell nuclei may usually be distinguished from the other types of nuclei though they vary considerably in size, but in smaller forms it is often not possible to identify all nuclei with certainty. In such cases one must place reliance purely upon considerations based on comparative anatomy. In the majority of instances no attempt has been made to trace the nerve fibers but the nerve cell pattern has been recorded and found to be of considerable value from the standpoint of comparative histology. In very large nematodes the nerve cells of the esophagus are often disproportionately small and may easily be overlooked. This seems a probable reason for the small number of such cells reported to occur in ascarids and spiruroids. In forms with multinucleate esophageal glands the nerve cells may be easily confused with gland nuclei. Of course, it is also possible that in such forms (always devoid of a valved bulb) there is no need for the complicated esophago-sympathetic system of smaller forms.

In *Spironoura affine* (Fig. 97A) there are seven cells in each nerve anterior to the nerve ring (Fig. 97P); two of these are glia cells ( $n_{1-3}$ ,  $n_{10-11}$ ), the remainder nerve cells ( $n_{1-3}$ ). The nerve fibers give off lateral branches (Fig. 97P) into the radial muscle regions. No further nerve cells are present in the procorpus. The metacarpus contains three large nerve cells in the dorsal nerve ( $n_{24}$ ,  $n_{26}$ ,  $n_{32}$ ) and five nerve cells in each subventral nerve ( $n_{22-23}$ ,  $n_{31-31}$ ,  $n_{33-34}$ ). At the base of the metacarpus we find a well developed commissure between  $n_{20-21}$  and  $n_{32-34}$ . The bulbar region (Fig. 97Q) contains nine cells attributable to the nervous system of which at least two ( $n_{11-12}$ ) and possibly a third ( $n_{35}$ ) are probably glia cells. There are two commissures in the bulbar region, an anterior and a posterior (Fig. 97A). The connection of the esophago-sympathetic with the central nervous system has not been observed for *Spironoura*. However, we presume it to be similar to that of *Ascaris* in which a process of each of the subventral nerves passes through the external wall of the esophagus near the level of the dorsal gland orifice (Fig. 97R). This process continues posteriorly on the outside of the esophagus connecting with a bipolar cell and through this cell with the nerve ring.

Goldschmidt recorded only 17 cells in this system in *Ascaris lumbricoides* in which Hsü recorded 18 cells; de Bruyn recorded 27 in *Angusticaecum holopteron* and Martini 20 in *Oxyuris equi*. All of these writers mention cells of dubious or unknown significance in the esophagus, particularly in the procorpus. Our own observations on *Ascaris lumbricoides* indicate that a set of six cells near the level of the dorsal gland orifice are homologous to  $n_{1-6}$  of *Spironoura*.

The peculiar distribution of nerve cells in representatives of the suborder Enoplina is worthy of particular note since it is very probably indicative of relationship. As may be seen from the diagrams (Fig. 90)  $n_{10-20}$  and  $n_{33-34}$  are usually marginal in position in the subventral sectors as are  $n_{30-31}$  in the dorsal sector. Together with  $n_{20}$  and  $n_{12}$  the latter nuclei form a quadrangle in forms such as *Tripyla papillata*, *Dorylaimus obtusicaudatus* and *Metoncholaimus pristiurus*.

## 3. FINER STRUCTURE OF THE ESOPHAGUS

**FIBERS.**—Considerable discussion has taken place as to whether or not the marginal fibers are contractile. Hamann (1895), Rauter (1907), Allgen (1921), Plenk (1924, 1925, 1926) and Looss (1905) maintained that the marginals are contractile, while Looss (1896), Schneider (1902), Goldschmidt (1904) and Martini (1916, 1922) hold that they are supporting or skeletal structures and observations of the writ-

ers support this view. In the marginal region of *Ascaris* one finds two types of fibers, a first type, extending from the esophageal lining to the esophageal covering, a second type extending longitudinally in two more or less distinct rows, one on each side of the esophageal margin. This second type, the "fiber plates" of Goldschmidt (1904), is known only in ascarids.

The radial fibers extend more or less perpendicularly from the esophageal lining to the external covering of the esophagus but often run rather obliquely so that their contraction might easily shorten the esophagus to a moderate extent. K. C. Schneider (1902) characterized the radial fibers as striated muscle. This view was supported by Martini (1916) though other authors including Goldschmidt (1904) disagree, stating that the appearance of striation is due to a minute system of supporting fibrils. Convincing evidence of striation of the muscle is not yet established. It is therefore concluded that if such is present, it must be of a rather peculiar character hardly comparable to striated muscle in other organisms.

Finally the "fenestrated membrane" described by Goldschmidt (1904), Kulmatycki (1918, 1922) and de Bruyn (1934) in ascarids shall be discussed. This is a longitudinal membrane between the external and the internal coverings of the esophagus beginning at some distance from the head, ending near the base of the esophagus. The writers find no indication of such a structure. However, Kulmatycki (1922) states that it is actually double and in places can be seen to be a distinct tube. He illustrates that which is obviously an esophageal gland tubule. Since the gland branches coincide with the location of the "fenestrated membrane," and since we can find no other structure fitting the description, the whole probably is a misinterpretation.

**DUCTS AND TUBULES.**—The internal structure of the esophageal glands has been very little studied and a generalization from the meager information available would be presumptuous. In the past the glands have been considered as rather simple structures, most investigators regarding the ducts as in direct continuity with the gland protoplasm. Actually, this is never the case. The esophageal gland ducts are continuous with tubules of various types. When the gland orifice is some distance from the actual beginning of the gland substance, there is a long unbranched central duct. This duct may continue after reaching the glandular region and give off lateral paired side branches, "pinnate branching." The terminations of the branches may be "tubular" or "alveolar (acinus)."

Hsü (1933) speaks of "simple tubular" glands in *Philometra* and *Dracunculus houteieri* stating that other nematodes have "branched tubular" glands. It is very easy to fall into error regarding such structures, particularly when the glands terminate in acini or branched acini. This is, in fact, the case in regard to the glands of *Dracunculus dahomensis*, the subventral ones being compound branched alveolar glands, while the dorsal is apparently of the simple branched alveolar type.

In forms such as *Ascaris lumbricoides* the dorsal gland is simple (pinnately branched); the subventrals are compound (palmately branched) and tubular. In *Physaloptera marillaris* all three glands are simple (pinnately branched) and apparently tubular (Fig. 98II). However, one has difficulty in tracing the secondary and tertiary tubules; they might easily terminate in acini. The compound form of the dichotomously branching tubular glands of dioctophymoids is obvious, as are the simple branched tubular glands of *Trichuris ovis* and *Agamermis decaudata* (Fig. 96).

Alveolar glands are particularly difficult to study. Preservation of the tubules in satisfactory condition for study is actually a rarity and for answer to many of the problems one must look to living specimens. Quite often the lobulations of the gland protoplasm itself are mistaken for the tubules. Such lobulation is dependent upon muscle distribution and may have no bearing on the tubular system (the stichocytes of *Trichuris ovis* and *Agamermis decaudata* have branched tubules though the glands are not highly lobulated).

**"CHROMIDIA."**—Working with *Ascaris lumbricoides* Goldschmidt (1904) described bodies in the plasma of the muscles associated with the radial nuclei. They stained intensely with hematoxylin and he termed them chromidia. These bodies he conceived to be "vegetative" nuclei originating from the radial nuclei. Vejdosky (1907) and Bilek (1909) considered them artefacts but Hirschler (1910, 1912) demonstrated their existence in the living cell. Neither Hirschler, von Kennitz (1912) nor Kulmatycki (1922) found any evidence that they originated from the nucleus. These bodies are found only in

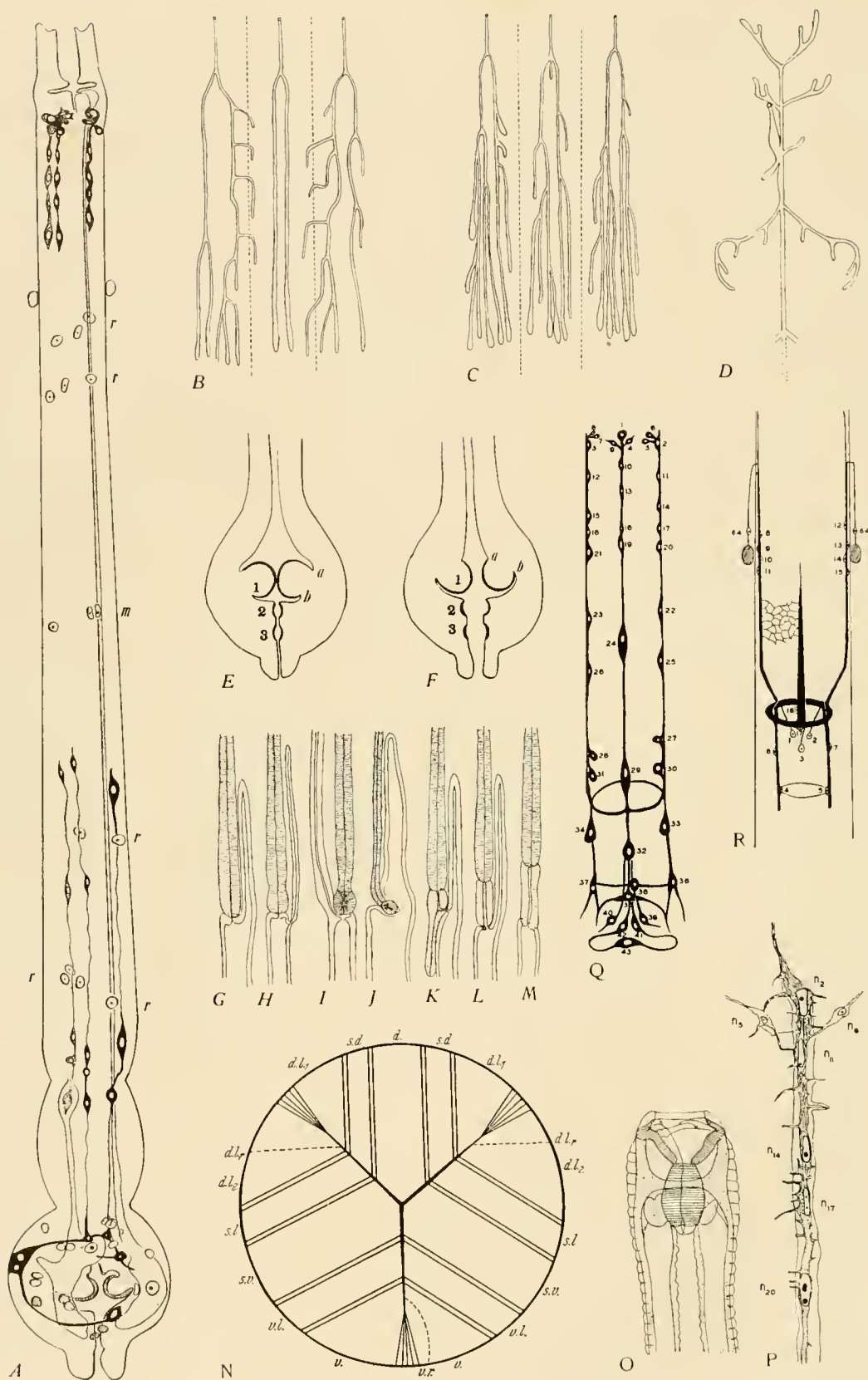


FIG. 97

A—Reconstruction of esophagus of *Spiranura* showing nuclei, glands and esophago-sympathetic. (Dorsal to reader's right.) B—*Dioctophyma renale*, esophageal gland tubule branching. C—*Saboliphyma haturini*, esophageal gland tubule. D—*Ascaris lumbricoides*, dorsal esophageal gland tubule. E-F—Rhabditoid bulb. (E—at rest; F—contracted). G-M—Ascaridid esophagi and intestines. (G—*Amphicacum*; H—*Angustiacum*; I—*Dujardinia halicarnis*; J—*Dujardinia helicina*; K—*Contracacum*; L—*Porrocaecum*; M—*Anisakis*). N—Diagram of esophageal symmetry. (d, dorsal area; dl, dorsolateral area of dorsal sector; dl<sub>2</sub>, dorsolateral area of subventral sector; dl<sub>1</sub>, dorsolateral (i. e., subdorsal) esophageal radius; sd, subdorsal area; sl, sublateral area; sv, subventral area; vl, ventrolateral area; v, ventral esophageal radius; v.r, ventral esophageal radius). O—*Oxyuris equi*, (Fourth stage larva). P-Q—*Spiranura affine*, esophago-sympathetic nervous system. (P—Diagrammatic connection of cells, dorsal view, compare with A.; Q—Detail of right subventral nerve trunk, lateral view). R—*Ascaris lumbricoides* (Esophago-sympathetic nervous system, diagrammatic dorsal view. D & N after Chitw. & Hill, 1932, Ztschr. Zellforsch., v. 14 (4). G-M, after Baylis, 1920, Parasit., v. 12 (3); O, after Ihle & Oordt, 1921, Proc. Sec. Sc. K. Akad. Wetensch. Amsterdam.



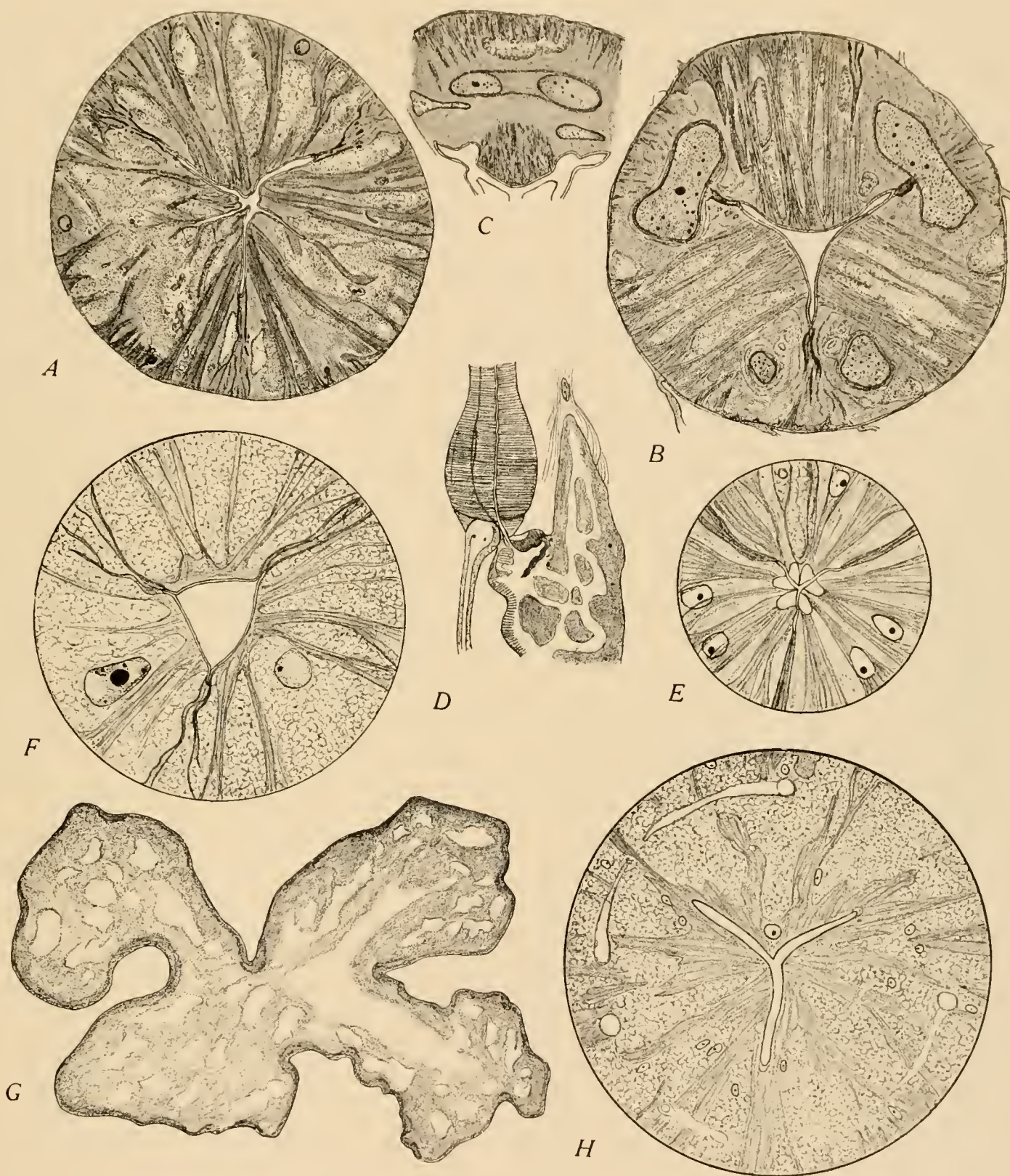


FIG. 98

A-C—*Ascaris lumbricoides*. (A—At level of subventral gland orifice; B-C—at level of esophageal gland nuclei [the dorsal gland nucleus is bilobed, lobes coming together in C]); D—*Goezia annulata* (Showing esophageal appendix left, and intestinal caecum, right, also connective tissue cell). E-F—*Camollanus microcephalus* (E—through corpus at level of first group of radial nuclei; F—glandular region at level of

subventral gland nuclei). G—Terminal part of dorsal esophageal gland tubule of *Ascaris lumbricoides*. H—*Physaloptera maxillaris*—(Glandular region, note 1 radial nucleus central in dorsal sector, numerous gland nuclei, and duct branching. A-C & G, after Chitw. & Hill, 1932, Ztschr. Zellforsch., v. 14 (4). D, after Hamann, 1895, Die Nemathelminthen, v. 2.



the large ascarids and are most numerous in the vicinity of the radial nuclei, but they may also occur in the marginal areas or at considerable distance from the nuclei. They vary in number and appearance. When few are present they tend to take the form of coiled fibers, and when many are present the form of thick flecks; both forms may be seen in a single chromidium. Kulmatycki (1922) found such structures as well as a golgi body in cells of the spicule sheath, thereby eliminating the possibility that the chromidia are homologues of the golgi body; he named them ascaridochondria, relating them to mitochondria, chondrosomes, etc. "Chromidia" occur in marginal areas of *Anonchus mirabilis* (Fig. 84 D-F), even more spectacularly than in *Ascaris*. Their significance, today, is unknown.

**OCELLI AND PIGMENT SPOTS.**—The occurrence of pigment masses in the Aphasmdia has been mentioned. That such structures exist, has been known since the time of Bastian. Because of their general appearance they have been widely accepted as photoreceptors despite a total absence of evidence that they are connected with the nervous system. Brownish to red granules may be rather irregularly and generally distributed in the esophageal tissue of such forms as *oncholaimus*. Similar pigmented granules may be slightly more concentrated in the subdorsal marginal areas of forms such as *Enoplus* and *Chromadora*. In these forms there is a definite pair of "pigment spots" but the pigment also extends posteriorly from the spots and may be present to a considerable extent in the subventral marginal regions of the esophagus. Rauther (1907) regarded the pigment granules of *Enoplus* and *Oncholaimus* as excretory granules and thought they were eliminated through the esophageal glands. We find no evidence of the "refractive granules" in the ducts of the esophageal glands and see no reason to assume they are excretion products. Schulz (1931b) upon finding the spots to be within the esophagus in *Enoplus* reaffirmed Rauther's interpretation and differentiated such bodies from true ocelli (with lenses) which he observed in *Leptosomatum*, *Thoracostoma* and *Parasymphlocostoma*. In the latter type he described the lens as an invagination of the superficial cuticle of the body surrounded by pigment and connected with a special ocellus cell. He states that he does not believe the true ocellus is connected in any way with the esophagus. On the contrary, the writers have found the ocelli of *Leptosomatum elongatum* to be completely enclosed within the wall of the esophagus; the lens seems to be formed from the external covering of the esophagus and no special cell is associated with the ocellus. We must conclude that even in this instance the ocellus is a part of the esophagus. If it is innervated, as one would presume, then the esophago-sympathetic nervous system must include also, the "optic nerve." In the Desmoscolicoidea, there is definite evidence that the pigment bodies are outside the esophagus; in this group the posterior part of the esophagus is degenerate and the esophageal glands outside the general contour. In *Monhystera paludicola* true ocelli are present; these are likewise situated outside the esophagus.

There remains one additional case of pigmentation in the cephalic region associated with photoreception. In the gravid female of *Mermis subnigrescens* Cobb (1926, 1929) described diffuse reddish pigment anterior to the nerve ring. Such pigment is absent from the head of young females and males, only being found in specimens ready to deposit eggs. Though the exact location of the pigment was not determined, the case is interesting since it supplied the only actual evidence of photoreception in a nematode, for egg laying only takes place in the light, ceasing in darkness. That heat is not the stimulus is indicated by the fact that such "egg laying" females will continue to lay eggs though placed on ice in a dish of water so long as the light continues.

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## CHAPTER VII

### THE INTESTINE OR MESENTERON

#### A. GENERAL MORPHOLOGY

The intestine of nematodes is a tube the wall of which is composed of epithelial cells. Its gross morphology does not vary markedly in different groups of nematodes. Usually it is a simple, more or less straight tube accommodating itself to the reproductive organs and space in the body cavity.

**SUBDIVISIONS OF INTESTINE.**—The intestine may be divided into three regions: the anterior part or ventricular region; mid-region or intestine proper; and the posterior part or prerectal region. The ventricular and prerectal regions commonly differ from the mid-region in the height of the cells and shape of the lumen. Usually, there is also some difference in the type of cell inclusions present in these regions. When a region is quite definitely differentiated from the remainder of the intestine it is herein termed either a ventriculus (anterior) or prerectum (posterior) while an adjectival usage is retained when the differentiation is not marked.

**APPENDAGES.**—Two types of cecae or diverticulae occur in the ventricular region, one directed anteriorly, the other posteriorly. The first type is by far the more common, occurring in various degrees of development in members of several groups in the Phasmodia. Only one free-living nematode is known with such a structure, namely *Rhabditis cylindrica*, and in this instance the cecum is very small, scarcely a third of the intestinal diameter in length. Likewise but one member of the Strongylina, *Grammocephalus* (Ancylostomatidae) has been described as possessing a short intestinal cecum and but a few representatives of the order Spirurida (*Dacnitis* spp. and *Dichelyne* spp.) have such structures. The cecae in these forms are quite small. Development of ventricular cecae is most common in the Ascaridoidea, sporadically occurring in such forms as *Contraecacum*, *Angusticacum* and *Amplicacum* (Ascarididae, Anisakinae). In the last mentioned forms the cecum may be very large (Fig. 97 G-M), extending far beyond the base of the esophagus, even to the nerve ring. A posteriorly directed cecum (Fig. 99D) is known to exist only in females of the genus *Leidyne* (Thelastomatidae).

No satisfactory explanation of the intestinal cecum development in nematodes has yet been made. The sporadic occurrence of this structure does not seem to be correlated with feeding habits. Phylogeny throws no light on the subject, for closely related forms may differ in this respect. Though the cecum is always a development of the ventricular region its cells do not differ cytologically from the remainder of this region, indicating no functional specialization (Fig. 98D).

**LAYERS.**—The intestinal wall consists of a single layer of epithelial cells which usually bear on their internal surface a bacillary layer (Stäbchensaum, *bordeur en brousse*), and some times a distinct subbacillary layer (Deckschicht) is apparent. The external surface of the cells may be quite naked, or it may be covered by a distinct basal lamella, a "muscularis mucosae," and a mesenterial membrane. One or more of these coverings may be present or they all may appear to be absent.

Sometimes the protoplasm of the epithelial cells is divisible into distinct zones. The ectoplasmic zone is a layer of dense cytoplasm bordering the sides of the cell; when definitely thickened on the side of the cell facing the lumen it is called a plasma cap (Fig. 103J3, Z3). The remainder of the cell is termed the endoplasm; it contains the nucleus, cell inclusions and sometimes other structures such as plasma strings (Fig. 103J5), basioplasm (Fig. 103J6), basal fibrillae, etc.

**The Bacillary and Subbacillary Layers.**—The bacillary layer consists of an internal border appearing to be made up of fine rods or "cilia" beneath which one often finds a subbacillary layer (Deckschicht) which stains with iron-haematoxylin. The first layer varies markedly in appearance, the bacilli sometimes being rather large and well separated, sometimes compact, sometimes fine and hair like. Under ordinary circumstances the bacillary layer has a compact appearance but the elements have been seen quite discretely in living specimens of *Rhabditis strongyloides*. In general, the bacillary and subbacillary layers are most highly developed (thickest) in representatives of the Strongylina (Fig. 102K) and impart a characteristic appearance which one is not likely to confuse with

that of other nematode groups. Sometimes due to fixation the bacillary layer may have pulled away from the epithelium, giving the appearance of a peritrophic membrane. Like the bacillary layer of other organisms it is digested by proteolytic enzymes and is therefore non-chitinous. (The peritrophic membrane of arthropods is chitin).

Somewhat extended discussions of the significance of the bacillary layer have been given in the past. Since this layer is not peculiar to the Nematoda, but occurs in the intestine of various groups of worms as well as in arthropods and vertebrates, conclusions based on the study of nematodes alone could scarcely be considered valid. The several viewpoints expressed have been as follows: (1) The bacillary layer is a development of minute tubes which aid in resorption or ex-

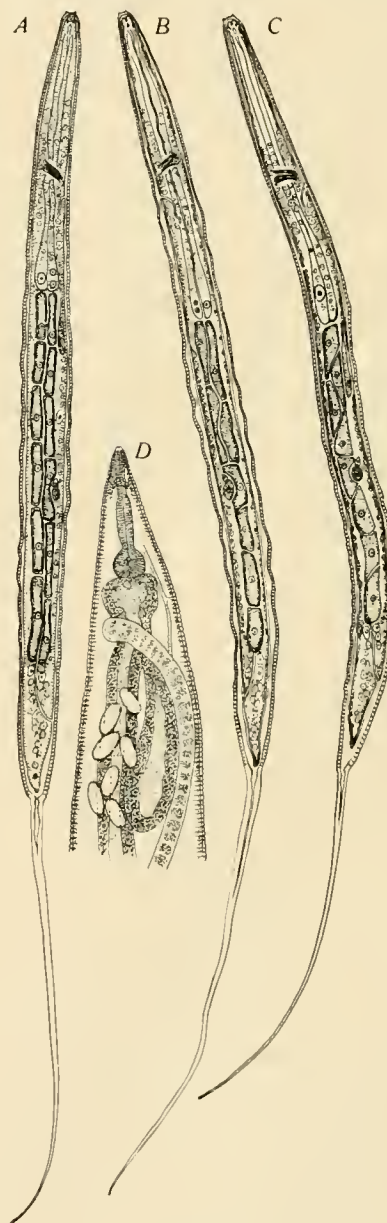


FIG. 99

A-C—Third stage larval strongyles showing oligocyt. (A—*Gyaloccephalus cupidatus*; B—*Cylicocercus goldi*; C—*Cylicocercus catinatus*). D—*Leidyne appendiculatum* (Adult female showing cecum). A-C, after Lucker, 1936, Proc. Helm. Soc. Wash., v. 3(1). D, after Chitwood, 1932, Ztschr. Parasitenk., v. 5(1).



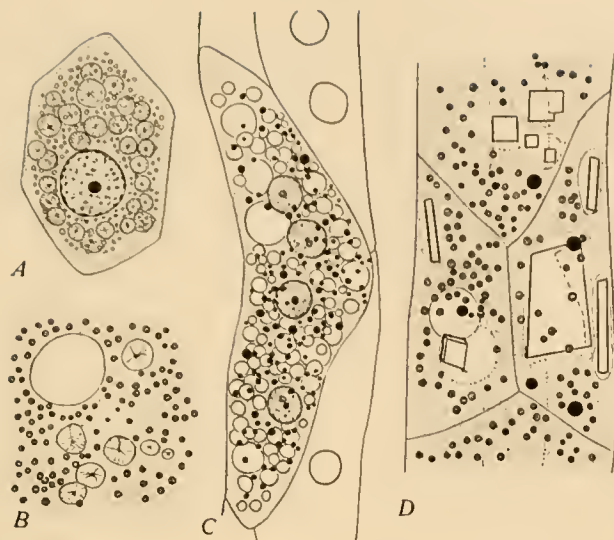


FIG. 100

Intestinal cell inclusions. A—*Rhabditis strongyloides* (Living intestinal cell, surface view; large radially striated rhabditin sphaerocrystals and small, soluble granules). B—*Theristus setosus* (Area of intestinal cell showing nucleus [not shaded], rhabditin sphaerocrystals, and olivaceous sphaeroids [small, shaded]). C—*Ditylenchus dipsaci* (Cell to left with four shaded nuclei, numerous colorless fat droplets and small black [actually purple] protein globules [stain, crystal violet]). D—*Diploscapter coronata* (fat globules black, olivaceous sphaeroids shaded, nucleus colorless, crystals colorless, in vacuoles [osmic]). Original.

FIG. 101

*Rhabditis monhystra*. Rhabditin sphaerocrystals as seen in polarized light. After Cobb 1914, J. Parasit., v. 1(1).

cretion; (2) it is itself a secretion product of protective nature; (3) it is a layer of amalgamated or degenerate cilia. The second possibility seems least probable in the light of comparison by which one finds the layer very well developed in forms which hold to a liquid or semiliquid diet (*Rhabditis*, *Trichuris*) and is absent in some forms with a "solid" diet (*Metoncholaimus*). Quack (1913), following Bütschli's alveolar theory of protoplasm, held the bacilli of the bacillary and subbacillary layers to be rows of vacuoles and not actual entities, while Hetherington (1923) held the bacillary layer to be cilia and the subbacillary layer basal granules. Upon the basis of appearance and comparative morphology one must conclude that Hetherington's view is the more probable. The function is a problem for general zoology rather than nematology.

**Protoplasmic zones.**—The presence of protoplasmic zones, likewise, seems to be of no special significance in nematology since differentiation into ectoplasm and endoplasm is of widespread occurrence in cells of living animals. Certain authors, such as K. C. Schneider (1902), have seen fit to call the plasma cap of *Ascaris* a "nutritrice zone." Quack has shown that in *Ascaris* such material is not confined to the periphery but extends into deeper parts of the cell as irregular masses (plasma strands) in *Ascaris* and may be so distributed as to form a mantle (Quack's fig. 21). Goldschmidt (1904) interpreted the strands as a "Chromidialapparat" but Hirschler (1910), von Kemnitz (1912), and Quack (1913) all have found this to be an error. Quack found that starved specimens of *Ascaris* showed no diminution in the plasma cap or plasma strands and hence eliminated the possibility that the material involved is absorbed albumen, concluding that it is differentiated functional ectoplasm (Compare Figs. 103J-M).

**External coverings.**—In large myriocytous (see p. 103) nematodes one often finds a homogeneous, slightly basophilic layer in immediate contact with the external cell surface, this layer being termed the *basal lamella* (Fig. 103J7, Z6). Apparently this layer is a differentiation acting as a supporting structure or it is a secretion product of the intestinal epithelium. It is not subdivided into areas corresponding to the cells and the ectoplasm is attached to it rather than continuous with it. Fibrillar strands of the ectoplasm reach its surface but do not appear to enter into it as one might expect if it were merely a differentiation of the outer cell surfaces. It acts more in the nature of a sheath and has affinity for collagen



stains. At the present time there is no actual proof that the basal lamella is formed by the intestine. Though such a layer is plain in *Ascaris*, *Physaloptera*, *Tanqua*, *Trichuris* and *Diocetaphyma*, in other forms it is generally not visible. The extent of its development is obviously not correlated with phylogenetic relationships but rather with cell numbers for in all of the above mentioned forms the intestine is myriocytous.

In most free-living nematodes one can discern no distinct mesenterial sheath over the intestine but in *Dorylaimus* as well as in the majority of parasitic nematodes an extremely thin membrane isolates the intestine from the body cavity and is termed the pseudocoelomic membrane (see p. 45). Beneath the membrane or mesentery, muscle fibers may be present but such fibers do not form a continuous layer and they are usually confined to the posterior part of the intestine (p. 42). However, in unusual instances they may form a coarse mesh work (Fig. 103H) which in cross section gives the appearance of a separate muscle layer. Such muscle fibers are classified as specialized somatic muscles rather than as a *muscularis muscosae*.

## B. MODIFICATIONS OF SUPERFICIAL APPEARANCE; FORM OF LUMEN

The superficial appearance of the intestine as observed in toto depends upon the total number of cells, the character of the cells and the character of cell inclusions. The shape of the intestinal lumen is likewise dependent on the number of cells, the form of the cells and whether or not they are equal or unequal in height.

**CELL NUMBER.**—Like the hypodermis and musculature, the intestine of various nematodes presents a series of stages in increased complexity; this series recapitulates to a greater or



a lesser extent the ontogeny of the individual. As long ago as 1866, Schneider called attention to the fact that strongyles have an intestine composed of but a few cells, 18-20, there being only two in a given intestinal circumference. Maupas (1900) noted that rhabditids also have but few intestinal cells in the adult stage, 30 being recorded in *Rhabditis elegans* while 18 were counted in newly hatched larvae of this species. Similarly Pai (1928) found only 18 intestinal cells in adult *Turbatrix aceti* and the writers find 64 intestinal cells in adult *Rhabditis strongyloides* and 20 in first stage larvae. On the other extreme we have forms such as *Ascaris lumbricoides* with innumerable intestinal cells (about 1,000,000), forms such as *Heterakis gallinae* with about 12,000 and intermediate forms such as *Prionchulus*, *Hystrignathus*, and *Metoncholaimus* with about 600, 400, and 5,000 respectively. In forms with 64 or less intestinal cells the most notable and obvious feature is that the cells tend to be longitudinally elongate and rectangular (Figs. 99A-C, 100C, 102C). When the number is 64 (Fig. 100A) the characteristic hexagonal appearance is first noticeable in only a few of the cells but when the number reaches 128 all are hexagonal.

The picture becomes clearer when this information is examined in the light of embryonic development. Martini (1903) found that when 10 cleavages have occurred the definitive larva is formed—an organism with a theoretic number of 1,024 cells. However, there is a definite lag of cleavages in the endodermal stem cell since the cells of this line actually number 16 to 20 instead of 128 as would be expected if no lagging occurred. Comparing this information with facts concerning the somatic musculature one notes that the tenth cleavage has taken place in the mesodermal stem cell since 64 cells are present at hatching, this being the total number to be expected, as well as the

typical number of cells in adult meromyarian nematodes. From this point of view, one might say that the course of regular cell division has not been fulfilled in a nematode with less than 128 intestinal cells and that cell division has only proceeded beyond "completion" when the intestinal cell number exceeds 128.

Thus, on the basis of the number of intestinal cells, one may classify nematodes into two groups, namely those which have not exceeded the "fore ordained" number and those which have exceeded this number. For the first condition we propose the term *oligocytous* while for the second condition the term *polycytous* may be used. However, there is a tremendous variation in the possible number of cells in the latter instance and for descriptive purposes a further division seems to be advantageous. Such a division is difficult but one finds a moderate correlation between the number and height of cells in a cross section and the total number of cells of the intestine.

Forms with less than 8,224 cells (16 cleavages) have more or less cuboidal epithelium with a maximum of 20-50 cells, usually of equal height, in a given circumference. Where raised areas occur in the lumen they are generally due to high individual cells. On the other hand forms with over 8,224 cells have 100 or more in a given circumference and definite plicae or villae are formed by groups of higher cells. The term *polycytous* is arbitrarily limited to forms with the former type of intestine (256-8,224 cells) while the term *myriocytous* is introduced for forms with the latter type of intestine (over 8,224 cells).

CELL CHARACTER.—It has previously been noted that cells in various regions of the intestine may differ in character; upon some occasions specialized cells may be scattered in the intestinal epithelium. Forms in which such cells are present

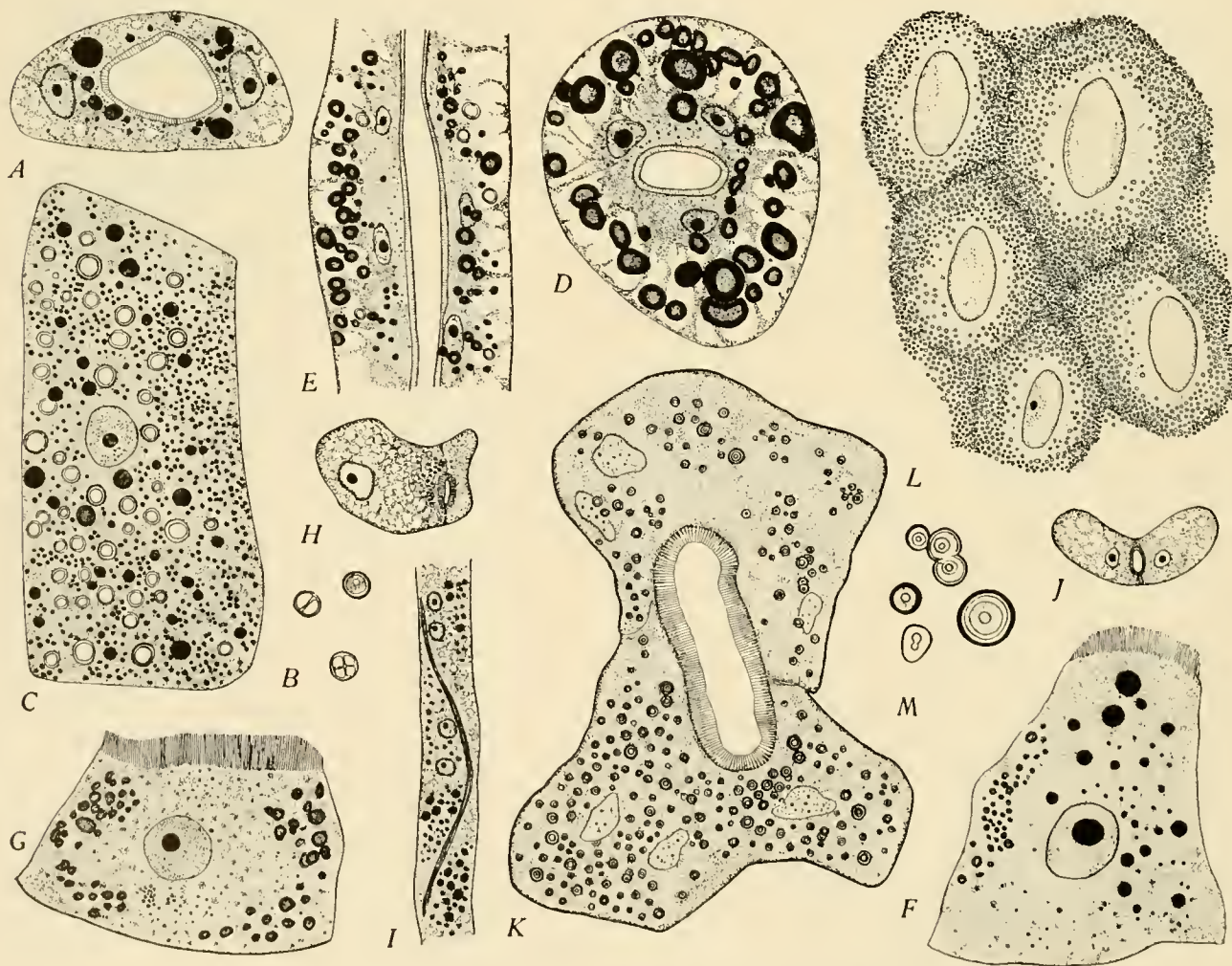


FIG. 102. INTESTINAL CELLS IN THE RHABDITINA AND STRONGYLINA

A-C—*Rhabditis terricola* (A—Cross, C—horizontal section of intestine; B—partially dissolved sphaerocrystals in neutral violet); D-E—*Panagrolaimus subelongatus* (D—Cross, E—longitudinal section of intestine); F-G—*Rhabdias eustreptos*. (Cells seen in cross section, F—

anterior, G—mid to posterior); H-J—*Ditylenchus dipsaci* (I—longitudinal section; H & J—cross sections); K—*Oesophagostomum dentatum* (Cross section); L-M—*Strongylus edentatus* (L—Surface view; M—isolated sphaerocrystals).



may be termed *heterocytyous* while forms in which the alternative is true may be termed *homocytyous*.

**CELL SIZE.**—The intestinal lumen may be rounded, sub-polygonal or quite irregular. A lumen of smooth contour occurs in oligocytyous forms, though even in such forms it may become irregular due to folds or rugae, involving the entire epithelial wall. A subpolygonal lumen is characteristic of polycytyous forms wherein each individual cell tends to cause a concavity in the outline of the lumen. Sometimes in *polycytyous* forms, but more commonly in *myriocytyous* forms, there are definite projections of cells into the lumen, such cells being taller than their neighbors; these groups of cells form villi or plicae (Fig. 103 E, F, I). This inequality in the height of cells in a given cross section may be termed *anisocyty* while the reverse would be *isocyty*.

**NUCLEAR NUMBER.**—As a rule intestinal cells in nematodes are uninucleate but exceptions to this rule are becoming more and more numerous with critical observation. The causes of polynucleation are not known; one can only interpret from scattered observations. Normal "Gigantism" of oligocytyous forms appears as one of the factors. Tremendous increase in cell size such as occurs in *Strongylus equinus*, where one finds single intestinal cells 4 mm long by 500  $\mu$  wide, apparently increase the requirements of nuclear material to such an extent that a uninucleate cell may be at a disadvantage. Given an equivalent amount of nucleoplasm many nuclei provide for more nuclear surface and a closer association of cytoplasm with nucleoplasm than could be obtained with a single nucleus. One might say that nemas inherently unable to continue cell cleavage compensate for this by undergoing nuclear division when natural forces no longer limit their size. Polynucleation is known to occur only in parasites. When characteristic of the entire intestine it is usually present in an entire natural group, but the exceptional sporadic cases (*Gnathostoma*, *Philometra*) are not explainable at present.

Increase in cell size in tylenchids can not be the cause of polynucleation since these forms are no longer than rhabditids. Quite obviously an insufficient amount of information has thus far been gathered to permit far reaching general conclusions.

Classifying nematodes according to the number of cells of the intestine, number of nuclei, specialization or lack of specialization, and equality or inequality of cells provides an interesting survey of the Nematoda. Examples of the known types are given in the accompanying table.

TABLE 1

Genus	Cell No. (1)	Nuclear No. (2)	Cell Size (3)	Cell Character (4)
Rhabditis	+	+	+	+
Ditylenchus	+	—	+	+
Chondronema	—	+	+	+
Strongylus	+	—	+	+
Rhabdias	—	+	+	+
Hystrignathus	—	+	+	+
Spironoura	=	+	—	+
Ascaris	=	+	—	+
Physaloptera	=	+	—	+
Tanqua	=	+	—	+
Gnathostoma	=	—	+	+
Philometra	=	—	—	+
Prionchulus	—	+	+	+
Metoncholaimus	—	+	+	—
Monhystera	+	+	+	+
Anonchus	+	+	+	+
Plectus	—	+	+	+
Halanonchus	—	+	+	+
Dorylaimopsis	—	+	+	—
Synonchiella	—	+	+	—
Tripyla	±	+	+	+
Leptosomatium	—	+	+	—
Enoplus	—	+	+	+
Ironus	—	+	+	—
Dorylaimus	—	+	+	+
Leptonchus	? +	+	+	+
Agameris	—	—	+	+
Trichuris	=	+	—	+
Diectophyma	=	+	±	+
(1)	(2)	(3)	(4)	
+ is oligocytyous	+ is uninucleate	+ is isocytyous	+ is homocytyous	
— is polycytyous	— is polynucleate	— is anisocytyous	— is heterocytyous	
= is myriocytyous				

## C. CELL INCLUSIONS

Under this heading are included all substances which are not a part of the active cytoplasm whether organic or inorganic, food reserves or waste products. Numerous types of stored food and waste products have been observed and in addition there is a residuum of non-classified material termed sphaeroids or granules. Food reserves are known to include glycogen, rhabditin, fats, and protein. Waste products are for the most part not classified chemically.

### (1) RESERVE FOOD MATERIALS

**Glycogen.** This substance, when present, is in a liquid or semiliquid state, since it is water soluble. In fresh material it may be identified through its coloration with iodine-potassium-iodide solution or the Best's carmine technique as described by Lee (1928). Giovannola (1936) has recently employed the new Bauer (1933) technique for staining glycogen in the intestine of preparasitic larval *Ancylostoma caninum*, *Necator americanus*, and *Nippostrongylus muris*. It is always best to use a saliva enzyme control, because that which is removed by saliva is presumptively carbohydrate in nature. Buseh (1905), von Kemnitz (1912) and Quack (1913) found glycogen to be the chief stored food in the intestinal epithelium of adult *Ascaris* and *Strongylus*. Giovannola reported glycogen to be the chief food reserve in the larvae of parasitic nematodes preceding and during rapid growth.

**Rhabditin.** This occurs as birefringent sphaero-crystals described by Maupas (1900), Cobb (1914) and Jacobs and Chitwood (1937) from the intestinal epithelium of *Rhabditis* spp. The sphaero-crystals are grey in color, bright spots in dark field illumination and bright spots with a central cross when observed between crossed Nichols of a polariscope (Figs. 100A-B & 101). They are slowly soluble in cold water, more rapidly on boiling; they are moderately soluble in 5% formalin, and in 10% acetic acid; rapidly soluble in dilute and concentrated hydrochloric, sulfuric, and nitric acids, in 50% formalin, and in sodium and ammonium hydroxides; they are insoluble in alcohol, glycerin, and xylol. When the intestines of specimens are mashed out under a cover slip and exposed to saliva or diastase at 37.5°C., these birefringents disappear from the intestine in one-half to one hour while approximately twice this time is necessary in water and in inactivated saliva controls. Iodine-potassium iodide has no effect. Presumably rhabditin is a carbohydrate but attempts to starve specimens and reduce the number of crystals were without effect. They disappear, however, when the larvae enter the encysted third stage (become "dauer" larvae).

Similar sphaero-crystals were described from the intestine of *Theristus setosus* by the writers (1938).

**Fats and Fatty Acids.** These substances are present as colorless globules imparting a grey opaque color to the organism. In dark field illumination they appear as bright circles, and between crossed Nichols they are not visible. Such material may be identified through its coloration with Sudan III, Scharlach R, Nile blue sulphate, osmic acid, and Flemming's Strong fixative. It is not dissolved by saliva, water, or hydrochloric acid and gives neither xanthoproteic nor ninhydrin reactions. It is, of course, soluble in alcohol, xylol and ether. Standard histological technique results in the appearance of large empty spaces or vacuoles wherever fats were present in the cell. Semipermanent mounts of small nematodes may be obtained by alcohol fixation, and evaporation to glycerin in Scharlach R or Nile blue sulphate according to the procedure of Goodey (1930). Pleasing temporary mounts can be made by placing living specimens in alcoholic solutions of Scharlach R. The most exact method is to cut the specimen, let the intestine flow out of the body and stain with Scharlach R, osmic acid or Flemming's fixative. If desirable they may be counterstained with haematoxylin. Permanent preparations may be made by sectioning osmicated specimens.

Von Kemnitz (1912) and Quack (1913) found fat globules in small amount in the intestine of adult *Ascaris* and *Strongylus*. Giovannola (1936) concluded that fat is the primary food reserve in larval parasitic nematodes in stages preceding a period of fasting. He further states that the quantity of fat globules is an index to the "physiological age" of preparasitic strongyloid larvae. More critical investigations along such lines would seem promising. Goodey (1930) identified fat globules in the intestine of representatives of the Tylenchidae, Rhabditidae, Diplogasteridae, Cephalobidae, Plectidae, and Mononchidae. The writers have identified fat as the chief form of stored food in *Cephalobellus* and *Blatticola* (Thelastomatidae), *Chondronema* (Allantonematidae), *Spironoura*

(Kathlianiidae), and various tylenchs, hoplolaims and criconematids and *Dorylaimus stagnalis*.

**Stored Protein.** Such substances occur as non-birefringent colorless globules similar to fat globules in transmitted light and dark field illumination. As described by Chitwood and Jacobs (1937), they are insoluble in water, alcohol, xylol, ether, and  $\frac{1}{2}$ -saturated ammonium sulphate; dissolve in 10% acetic acid and in 5% KOH; are not affected by saliva; are pale yellow in Flemming's fixative; give positive xanthoproteic and ninhydrin reactions; and are digested by artificial gastric juice. The globules stain with gentian violet or haematoxylin; they also stain blue with Nile blue sulphate and orange with Scharlach R. These reactions apparently place them as complex proteins of a conjugated nature. The majority of globules of *Agamermis* are composed of this type of substance and not fats as is commonly supposed. Similar globules have been identified by the writers (1938) in the intestine of *Ditylenchus dipsaci* (Fig. 100C). It is quite possible that the colorless, insoluble (in alcohol-xylol), basophilic globules, present in *Rhabditis*, *Panagrolaimus*, *Aphelenchoides* and *Plectus* etc., are of the same nature. The fact that such globules stain with Nile blue sulphate in the same manner as fatty acids indicates that staining technics are not necessarily indicative of fat. Proteins may stain as do fats but they may be distinguished through their insolubility in fat solvents, digestion in artificial gastric juice, and positive xanthoproteic and ninhydrin reactions.

## (2) WASTE PRODUCTS

**Inorganic Sphaero-crystals.** Reddish-brown, weakly birefringent sphaero-crystals occur in the intestine of many parasitic nematodes, including *Ascaris*, *Camallanus*, *Strongylus*, *Ancylostoma*, and *Trichuris*. These structures are similar in appearance to rhabdites both in transmitted light and between crossed Nichols, although in totemount preparations and sections they are not birefringent. The optical activity in this case can only be observed when the crystals are isolated. Unlike rhabdites, they are dark in dark field illumination and are insoluble in water, acetic acid, NaOH (all concentrations) and saliva. They are also insoluble in alcohol and xylol and are not affected by gastric or pancreatic enzymes. Askani (1896), Looss (1905) and Fauré-Fremiet (1912) regarded them as products of haemoglobin resorption, while Lièvre (1934) was unable to establish the presence of haemoglobin in the intestine of *Ascaris lumbricoides* and *Parascaris equorum* by spectroscopic analyses. He demonstrated the presence of haemoglobin by this means in 75% of the specimens of *Torocara canis* examined. Von Kemnitz (1912) identified them as zymogen granules and Quack (1913) identified them as gypsum ( $\text{CaSO}_4 \cdot 2\text{H}_2\text{O}$ ). The writers find that these crystals may be obtained relatively pure by boiling the intestine in 10% KOH and washing in a centrifuge. Crystals prepared in this manner are not charred by heating on a glass slide to the melting point of glass. They may be dissolved by heating in concentrated HCl and when cooled recrystallize in the general habit of  $\text{CaSO}_4 \cdot 2\text{H}_2\text{O}$ . Such crystals are birefringent and obliquely extinct. This is presumptive evidence that they are gypsum. However, a reddish-brown residue is left when the slide is dried. This residue stains blue in dilute HCl-potassium ferrocyanide, indicating the presence of iron; direct experiments on the sphaero-crystals produces the same result in partially dissolved (swollen) crystals. Some compound containing iron is evidently present as an adsorption within the sphaero-crystals. As evidence of the association of sphaero-crystals with a blood feeding mode of life, Törnquist (1930) pointed out that *Camallanus*, which is known to feed on blood, has them, while *Caecillanus*, which does not feed on blood, does not possess them. One might add that adult oxyurids and thelastomatids, as well as the first three larval stages of *Strongylus*, and *Camallanus* are also devoid of them. The evidence is entirely circumstantial. The occurrence of grossly similar insoluble sphaeroids in the intestine of *Theristus setosus* (see Olivaceous sphaeroids) and other free-living nematodes casts some doubt

on the above interpretation since they also contain iron. Lièvre (1934) interprets positive tests for iron in the intestine of *Ascaris* as due to substances obtained from animal and vegetable food, not haemoglobin.

**Olivaceous sphaeroids.** Reddish brown, apparently non-birefringent sphaeroids were observed by the writers (1938) in the intestinal cells of *Theristus setosus* (Fig. 100B). They have the following characteristics: Not blackened by osmic acid; not colored by Scharlach R, insoluble in alcohol; ninhydrin and xanthoproteic reactions negative; blue in neutral violet; blue in crystal violet, blue in Nile-blue sulphate; not digested by artificial gastric juice or diastase; soluble in 10% HCl and 2% KOH but not in 10% acetic acid or 2% HCl; blue in potassium ferricyanide followed by 1% HCl. From these observations it seems that the sphaeroids must consist of an organic ferrous iron salt or a salt of a weak base ( $\text{Fe}(\text{OH})_2$ ) and a weak acid. Similar sphaeroids were also observed in *Dorylaimus stagnalis* and an unidentified oncholaimid and *Diploscapter coronata* (Fig. 100D).

**Crystals.** Stefanski (1916) and Cobb (1918) observed polyhedral colorless birefringent crystals in the intestine of *Ironus*. They are very similar in appearance (Fig. 105P) to triple phosphate, and, according to Stefanski, they are very soluble in acetic acid and potassium hydroxide; slightly soluble in hot water and insoluble in cold water, alcohol, ether, chloroform, and acetone; are not stained by iodine-potassium-iodide, but stain with eosin and fuchsin. Isolated colorless polyhedral crystals have also been observed in *Tripyla* (Fig. 105A).

Crystal aggregates in mermithids were observed by Meissner (1853), Rauter (1906), Hagmeier (1912) and Christie (1936). These are first seen in vacuoles of the post-nodal region of preparasitic larval *Agamermis decaudata*. Their number increases with age and in old adult specimens similar crystals have been observed in the body cavity. They are very similar in appearance (Fig. 107D) to uric acid and allantoin; are birefringent, obliquely extinct; insoluble in water, alcohol, ether, 10% ammonium hydroxide, 10% acetic acid, 10% HCl, glycerin, and  $\frac{1}{2}$  saturated ammonium sulphate. Presumably they represent a nitrogenous product.

In *Diploscapter coronata* large quadrate tablets, colorless to yellowish brown, have been observed by the writers (Fig. 100D). Like olivaceous sphaeroids, they are non-birefringent, soluble in 2% sodium hydroxide and 10% hydrochloric acid but are insoluble in 1% HCl, alcohol and glycerin. They give a negative ninhydrin reaction and a positive potassium ferricyanide—1% HCl reaction. Therefore they appear to be a ferrous iron compound, probably organic in nature. It is possible that they may be crystals of the same substance composing the olivaceous sphaeroids.

## (3) MISCELLANEOUS "GRANULES"

In the majority of instances the cell contents of the nematode intestine have not been studied chemically. The term "granule" is, of course, chemically meaningless. Since at least four distinct substances are known to exist in a sphaeroidal state, namely, rhabdites, fat, protein, gypsum and olivaceous sphaeroids each form must be considered with care. With living specimens, dark field illumination is sufficient to separate the globules of fat and protein from the sphaero-crystals of rhabdites and gypsum. In addition, the first two are colorless while the last three are yellowish brown to reddish brown. However, still other types may be discovered. Non-birefringent brownish or yellowish refractive "granules" are present in the intestinal epithelium of *Metoncholaimus*, *Siphonolaimus*, *Ironus*, and other forms. Such "granules" are strongly refractive and non-staining (? olivaceous sphaeroids). In addition one finds moderately refractive basophilic "granules" in the intestine of such forms as *Dorylaimopsis*, and *Plectus*, and special cells of the intestine of *Synonchiella*. Cobb (1922) has described birefringent sphaero-crystals in special cells of *Eurystomina* as "marionellin" and we find these to be relatively insoluble and basophilic. In other forms acidophilic "granules" have been observed. For morphologi-

FIG. 103. INTESTINE IN ASCARIDINA, SPIRURINA AND CAMALLANINA

A—*Rhigonema infecta*. B C—*Spironoura affine*. (B—cross; C—longitudinal in prerectal region showing parasites). D—*Heterakis gallinae*. E-F—*Oxyuris equi* (E—superficial; F—longitudinal). G-H—*Macracis monoxystera* (G—cross; H—superficial). I—*Anisakis* internal view showing ridges as seen in dissection. J-Q—*Ascaris lumbricoides* (J—normal; 1. bacillary layer; 2. subbacillary layer; 3. plasma cap; 4. endoplasm; 5. plasma string; 6. basophilic; 7. basal lamella; K—binucleate cell, one nucleus degenerating; L—early cytoplasmic degeneration; M—late cytoplasmic degeneration; N—normal nucleus; O—early degenerating nucleus; P—mid degenerating nucleus; Q—late degenerating nucleus). R-S—*Torocara canis* (R—

intestinal cell with Cajal silver; S—with iodine vapor, glc. glycogen, grn i insoluble granule (sphaero-crystal). T-U—*Gnathostoma spinigerum*. V—*Rictularia coloradiensis* (grn b basophilic granule). W-Y—*Philometra rubra* (W—surface view; X—ventricular region; Y—mid region). Z—*Physaloptera retusa* (1. Bacillary layer; 2. sub-bacillary layer; 3. plasma cap; 4. endoplasm; 5. plasma string; 6. basal lamella). AA—*Tanqua tiara*. BB—*Ascaraphis* (*Cystidicola harwoodi*). CC—*Camallanus americanus*. E-F, after Martini, 1916, Ztschr. Wiss. Zool. v. 116; 1. after Cobb, 1888, Beitrage zur Anatomie und Ontogenie der Nematoden; R-S, after Argeseanu, 1934, Compt. Rend. Soc. Biol. v. 116; remainder original.



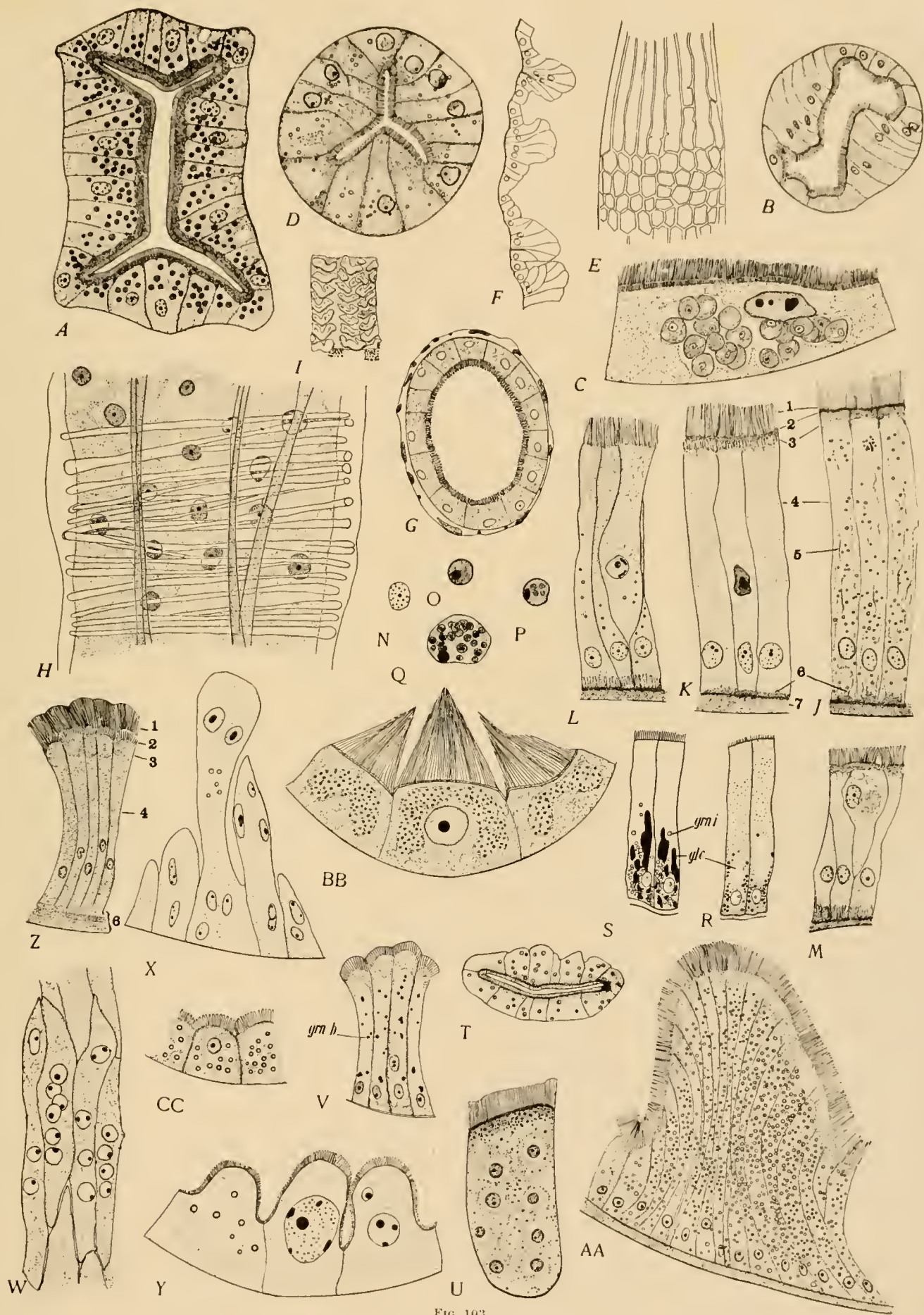


FIG. 163



cal purposes the term *globule* will be restricted to those inclusions which are known to be non-birefringent and appear as bright circles in dark field illumination, i.e. fats and proteins. The term *sphaerocrystal* is restricted to inclusions known to be birefringent, while *sphaeroid* is applied to strongly refractive non-birefringent or apparently non-birefringent bodies, and *granule* is reserved for moderately or weakly refractive bodies of unknown optical activity. It will appear obvious that weakly birefringent substances such as gypsum may easily be classified as sphaeroids pending critical study.

The function of gypsum, sphaeroids, and granules is for the most part unknown. Sphaerocrystals of gypsum were seen to be thrown out or "excreted" from the cells of *Ascaris* and *Strongylus*. The yellowish brown sphaeroids of *Rhabdias* and *Iranus* were also observed to be eliminated from the intestine (Fig. 105R).

#### (4) INTESTINAL PARASITES

Protozoan parasites are apt to occur in the intestinal cells as well as in other organs of nematodes and might easily be confused with cell inclusions or degenerating cells. Micoletzky (1922) described sporozoan parasites of the intestinal wall of *Dorylaimus carteri* and *Plectus cirratus*, and Kudo and Hetherington (1922) described a microsporidian named *Thelohaninia reniformis* from the intestinal epithelium of *Mastophorus muris*. The writers have encountered similar forms (Fig. 103C) in the intestine as well as the musculature, gonads, and chords of *Spironoura affinis*. It is sufficient, for the present, to merely call attention to their existence. Many protozoan and fungous parasites of nematodes have been described and such information will be presented in a later part.

### D. COMPARATIVE MORPHOLOGY

Up to the present time no consistent attempt has been made to record, much less present, specific information regarding the intestine in the various groups of the Nematoda. All workers recognize various impressions upon which they may have an "intuition" as to the group to which a nematode may belong. Whenever it is possible, in morphology, to reduce these sensory impressions to words, it invariably contributes to our understanding of relationships and to the transfer of knowledge from one worker to another. The present writers must of necessity deal in terms of examples. By giving a sufficient number of examples, it is hoped that a skeleton outline may be provided around which others can build a structure of some value.

*Rhabditina*. For the members of the Rhabditina we have the observations of Maupas (1900), Cobb (1914), Goodey (1930), and Giovannola (1936) as our only direct attacks on the problem, but numerous observations from the time of Butschli, preserved chiefly in the form of drawings, serve as a foundation upon which we may build.

The Rhabditina may be characterized as oligocytous, homoecytous, and isocytous with the exception of the Rhabdiasidae, Drilonematidae, and Allantonematidae, which appear to be wholly or in part polycytous. *Rhabditis* (Fig. 3, 100A, 101, 102A-C), *Turbatrix*, and *Diplogaster* retain the simple uninucleate condition in the intestinal epithelium. In these forms the cellular outlines are distinct and quite often emphasized by the absence of cell inclusions. The intestinal lumen tends to be flattened; the cells alternate, giving a zig-zag appearance in lateral view. Free-living stages of the Rhabdiasidae are also oligocytous, and in general quite similar to *Rhabditis*, while the parasitic adult is very definitely polycytous, the cells cuboidal (Fig. 102F-G). Ventricular and prececal regions are almost always differentiated from the remainder of the intestine through absence of, or marked diminution of, cell inclusions. The intestine cells of many species of *Rhabditis* contain birefringent sphaerocrystals of rhabditin, but this substance has not been identified in any other members of the suborder. Sphaeroids, apparently non-birefringent or weakly birefringent, are very noticeable in the parasitic female of *Rhabdias* but these are of the insoluble type. Anteriorly the intestinal circumference consists of about 12 cells, very low, containing few or no inclusions. In the mid-region there are six to eight somewhat higher cells containing a moderate number of small sphaeroids, numerous larger basophilic globules and small basophilic granules (Fig. 102F), while posteriorly the sphaeroids are larger, more numerous, and the basophilic bodies minute and numerous (Fig. 102G). In these forms the sphaeroids are a deep red-brown in color.

Maupas (1900) noted that in some species of *Rhabditis*

birefringents are absent. In such forms he found "albumino-fatty" globules to be more prevalent.

Cephalobids are usually described as having an intestine composed of two series of cells (rows). Though the lumen is dorsoventrally flattened and often appears zig-zag, as in *Rhabditis*, no cell walls are distinguishable in sectioned *Panagrolaimus subelongatus* (Fig. 102E). The nuclei are near the lumen, two to six, and usually four, in a given circumference, with a total of about 210. Since disappearance of cell walls occurs in the fourth stage larva, at the same time as nuclear division (there are about 20 uninucleate cells in the third stage larva), it seems best to interpret this form as primarily oligocytous, secondarily polynucleate and/or syncytial. Perhaps polynucleate cells will eventually be distinguished as in tylenchids. The cephalobid intestine in section is characterized by its large faintly basophilic globules, scattered brownish shells, and large empty spaces which presumably were filled with fatty substances.

The Tylenchoidea present a picture in contrast to the Rhabditoidea when the intestine is considered. Although Debray and Maupas (1896) were able to distinguish 16 cells forming the intestine of *Ditylenchus dipsaci* in the fourth stage larva, distinct cells have seldom been observed in the adult members of the Tylenchidae. The intestine appears as an opaque mass of large globules, very beautiful in dark field illumination, but not visible in polarized light. This material is of a fatty character. Sections of *D. dipsaci* and *Aphelenchoides parietinus* fail to show clear evidence of cell walls (Figs. 102H-J) in the adult stage. In dissected specimens the large quadrinucleate cells are seen (Fig. 100C). The cytoplasm is highly vacuolate due to the removal of fats. Basophilic globules are also seen in sections, but these appear to be very erratic in disposition. In *D. dipsaci* the lumen is dorsoventrally flattened anteriorly and zig-zagged posteriorly (Fig. 102H-J); 56 nuclei were counted in one specimen. In *A. parietinus* the intestine is quite similar except that its sides in the mid-region tend to be more nearly equal and tend to surround the gonads. In this form a maximum of two nuclei has been observed in one section and on one side of the intestine. It is notable that the lumen is relatively much smaller in tylenchids than in rhabditoids, and the bacillary layer relatively shorter and more compact. Apparently we have no increase in the number of intestinal cells, 16, between hatching and adulthood. In *Chondronema passoli*, the only representative of the Allantonematidae studied, the intestine is definitely polycytous, there being four to six hexagonal cells in a circumference. The cells are filled with fat globules as in the tylenchids. Unlike the latter, however, no bacillary layer appears to line the round intestinal lumen. The lumen contains a glassy-appearing substance, possibly of protein nature, which is slightly basophilic and apparently represents partially digested body fluid from the host. Aside from the presence of a few birefringents (nature unknown) in the posterior end of the intestine of *Chondronema*, there is no known case in which either ventricular or prececal regions differ from the mid-region in members of the Tylenchoidea.

*Strongylina* (Figs. 99 & 102). The Strongylina as a group appear to be oligocytous or low polycytous and the cells are polynucleate as noted in *Strongylus* by Schneider (1866), Looss (1901) and Quack (1913) and in *Ancylostoma* by Looss (1905). Other representatives of the same suborder (*Stephanurus*, *Oesophagostomum*, *Ostertagia*, *Longistriata*, *Metastrongylus* and *Dictyocaulus*) examined by the writers exhibit the same characteristics. The intestine consists of two rows each of 10 or more cells, each cell containing 10 to 500 nuclei. The smaller numbers, 10 to 20 nuclei, occur in members of the Trichostrongyloidea. In such forms as *Ostertagia* there are two rows of nuclei in each intestinal cell, four in an intestinal circumference while in *Trichostrongylus instabilis* Looss (1895) found each of the two cell rows of the intestine to contain a single row of nuclei. About 40 to 50 nuclei are present in an intestinal cell of *Oesophagostomum*, 500 in one of *Strongylus* while no reliable estimate has yet been made for *Metastrongylus*. The shape of the lumen is quite diverse, being dorsoventrally flattened in *Ostertagia*, irregular due to longitudinally folded walls in *Stephanurus*, or rounded to ovoid in *Oesophagostomum* and *Metastrongylus*. A thick, compact bacillary layer resting on a well developed subbacillary layer is characteristic of the Strongyloidea. Wetzel (1931) and Lucke (1935, 1936, 1938) have made use of the specific intestinal cell constancy of the third-stage larvae of horse strongyles as a means of differentiating the species in this stage. Thus Wetzel found two rows of eight long subtriangular cells in *Strongylus equinus*, two rows of ten cells in *S. edentatus*, and two rows of 16 cells in *S. vulgaris*. Lucke found a total of only eight cells in the intestine of *Cylicodontophorus*



*ultrajectinus*, *Cylicocercus goldi*,\* and *C. cutinatus* larvae, of 12 in *Gyaloccephalus capitatus* and of 16 in *Poteroostomum ratzii*. Similar identification of species of strongylin parasites of sheep has been shown practicable by Dikmans and Andrews (1933) on the basis of the intestinal cells of the third stage larvae.

Intestinal nuclei of strongylins are sphaeroid in such extremely divergent forms as *Ostertagia* and *Strongylus* while in *Oesophagostomum*, *Stephanurus*, *Ancylostoma* and *Kalicephalus* they are irregularly elongate or even tuboid. There is usually a slight, though distinct, diminution in the number of insoluble sphaero-crystals both in the ventricular and prececal regions of members of the Strongylinae; in such regions the lumen is often slightly larger and the epithelium thinner than in the remainder of the intestine. Glycogen, stored in the endoplasm, appears to be the chief food reserve. Like tylenchoids, however, there is relatively little absorptive surface in the strongylin intestine.

*Ascaridina* (Fig. 103). The Ascaridina present a very different picture for this group is polycytous to myriocytous. Polynucleate cells are rare; they never constitute more than a small proportion of the intestinal cells in a species. Insoluble sphaero-crystals appear to be absent in the Oxyuridae, Thelastomatidae, and Kathlaniidae while they are present in members of the Rhigonematidae, Heterakidae, and Ascarididae. The smaller representatives of the Thelastomatidae (*Blatticola*, *Cephalobellus*) and Oxyuridae (*Macracis*) are polycytous and isocytous while larger oxyuroids such as *Oxyuris equi* and *Enterobius vermicularis* as well as rhigonematids, kathlaniids, heterakids, and ascaridids are myriocytous and anisocytous. Distinct ventricular enlargements are characteristic of the polycytous oxyuroids such as *Macracis*, *Blatticola*, and *Cephalobellus* though such may also occur in some myriocytous forms such as *Heterakis*. In addition sections of the intestine of polycytous oxyuroids (also *Spironoura*) show numerous large vacuolate areas which correspond to fat globules seen in the living specimens. Passing to the myriocytous forms we find the ventricular region less and less apparent with increased cell number. There is also a marked tendency toward anisocety manifesting itself in *Rhigonema* by the formation of an oblong lumen; in *Spironoura* by an I-shaped lumen formed by

two staggered longitudinal ridges (Mackin, 1936) and in *Heterakis* by a triangular lumen or three longitudinal ridges (Baker, 1936). Tuft or villus formation has been described as a further development of anisocety in *Oxyuris equi* by Martini (1916); in this instance the tufts which are composed of numerous cells may give a hexagonal appearance when seen in toto (Fig. 103E). Jagerskiöld (1893, 1894) described groups of elongate cells especially developed in the anterior part of the intestine of *Contracaecum spiculigerum*, of *C. osculatum* and *Raphidascaris decipiens*; such cell groups reduce the lumen to a narrow, folded canal. Similar cell groups, according to Cobb (1888), take the form of V-shaped ridges (Fig. 103I) in *Anisakis simplex*. Anisocety in *Ascaris*, on the other hand, is limited in such a manner that the small cells are lateral and the lumen, consequently, takes the form of a dorsoventrally flattened tube (Fig. 500). Glycogen constitutes the chief stored food in *Ascaris* according to Kennitz (1912) and Quack (1913) while glycogen is absent in *Oxyuris* according to Martini (1916) and this is in agreement with the writers' findings that fatty substances are the energy reserves of oxyuroids while appearing in negligible quantity in ascaridids.

Polynucleate cells with two to three nuclei have been observed upon rare occasions in *Spironoura* but they appear to be quite common in the lateral areas of the intestine of *Ascaris*. Ehrlich (1909) associated polynucleation in *Ascaris* with nuclear degeneration but Quack (1913) was unable to substantiate this view. Rather extensive studies of both nuclear and cytoplasmic "degeneration" have been made with this form by Ehrlich, Quack, and Guieysse-Pellissier (1909). Nuclear degeneration involves an enlargement of the nucleus, increased basophilia and the formation of strongly refractive sphaeroids (Fig. 103N-Q) within the nucleus; these changes are followed by elimination of the cell, or a portion of the cell containing the nucleus, into the intestinal lumen. So-called cytoplasmic degeneration (Fig. 103M) involves the formation of an acidophilic mass, usually near the base of the cell, inclusion of normal cytoplasmic sphaero-crystals within the mass, movement of the whole toward the lumen and final elimination. Martini (1916) illustrated such elimination of "degenerate cells" in *Oxyuris*. The regularity of the occurrence of "degeneration" in *Ascaris* leads one to suspect that it is a normal physiologic process not necessarily retrogressive in nature. Assuming that insoluble sphaero-crystals are waste products, "cytoplasmic degeneration" might be considered a mode of excretion. In *Rhabdias* and *Strongylus* it has been

\*Regarding *Cylicocercus goldi* Lucker (1938) states that the lumen passes between the first three cells "through the cytoplasm of the five posterior cells." He assures us that there are only 8 nuclei and 8 cells in the third stage larvae. It still seems possible that he may have overlooked something. Compare figs. 100 C, 102 H-J, and figs. 99 C.

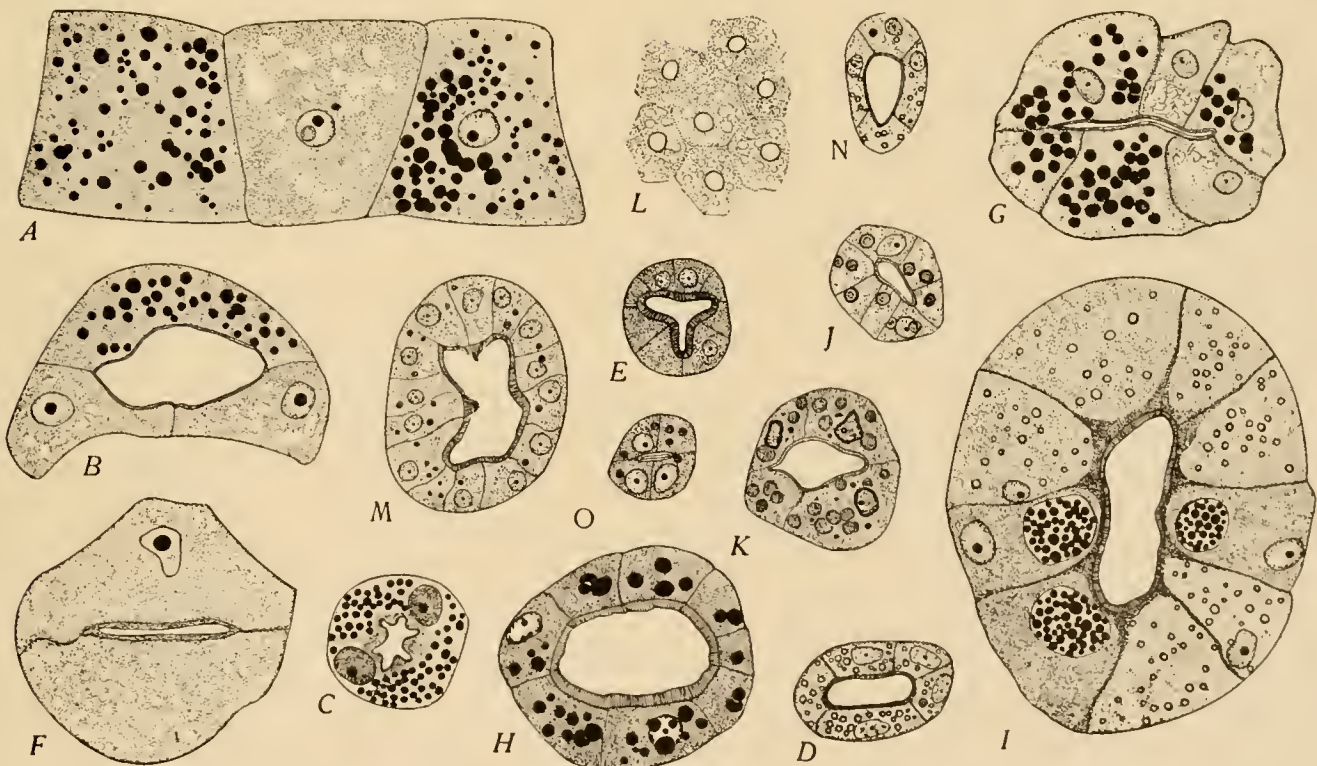


FIG. 104. INTESTINE IN CHROMADORIDA

A-B—*Synonchiella truncata*. C—*Monhystera camburi*. D—*Axonolaimus spinosus*. E—*Wilsonema bacillivorus*. F—*Tripylium carcinicolum* s. *calkinsi*. G—*Dorylainopsis metatypicus*. H—*Anaplectus granu-*

*losus*. I—*Halichoanalaenus robustus*. J—*Ethmolaimus revatiensis*. K—*Anonchus mirabilis*. L—*Chromadora* sp. M—*Halalanonchus macramphidum*. N—*Chromadora* sp. O—*Chronogaster gracilis*. Original.



previously noted that sphaerocrystals are normally eliminated in the faeces.

*Spirurida* (Fig. 103). For the order Spirurida there is a surprising dearth of recorded knowledge concerning the intestine. Jägerskiöld (1893, 1894), Magath (1919), Hetherington (1923) and Törnquist (1931) seem to have been the only authors who gave the intestine consideration. It is peculiar that in this group there appear to be as many instances of marked dissimilarity of the intestine in closely related forms as there are instances of similarity. All of the members of this order appear to be myriocytous with the possible exceptions of *Gnathostoma* and *Philometra*; the latter have relatively few, large, polynucleate cells (Fig. 103U & W). Insoluble sphaerocrystals are present in *Philometra*, *Dracunculus*, *Micropleura*, *Camallanus*, *Gnathostoma*, and *Tanqua*, while they are absent in *Ascarophis* (*Metabronema*), *Cucullanus*, *Physaloptera* and *Rictularia*. Basophilic globules, probably of a protein nature, are present in *Rictularia*. Most of the representatives of this group have very tall, narrow intestinal cells and are anisocytous because the epithelium exhibits either longitudinal ridges and valleys or villi. However, three forms are conspicuous exceptions to this rule, namely, *Camallanus*, *Ascarophis* and *Gnathostoma*. Diversity in height of cells and character of the bacillary layer and basal lamella are also conspicuous features of the group.

*Chromadorida* (Fig. 104). In the Chromadorida the only observations regarding the intestine have been of an incidental nature. We have records such as those of de Man (1884) in which species of the genus *Monhystera* are differentiated on the basis of their having a black or grey intestine and "two cell rows" or more than two cell rows. The rich red-brown to black pigmentation of the intestine of *Siphonolaimus* was recorded by zur Strassen (1904). The number of cells in an intestinal circumference was mentioned by Cobb (1920) in many forms of this group. Zur Strassen (1904) and Schepotieff (1908) were the only previous workers to study sections of forms of this order.

Members of the family Plectidae have relatively few intestinal cells, 120 to 930, the form with the smallest number, *Anonchus*, being oligocytous while the remaining forms studied, *Plectus*, *Chronogaster*, and *Wilsonema* are polycytous. *Anonchus* and *Chronogaster* have only four cells in a circumference, a very low bacillary layer, flat lumen, and large eosinophilic granules. *Wilsonema* has up to eight cells in a circumference, a lobed lumen, high bacillary layer and no granules and *Plectus* has up to 12 cells, a rounded lumen, high bacillary layer and basophilic globules (? protein).

In the family Camacolaimidae, *Aphanolaimus* has around 100 cells (oligocytous), a flat lumen, a high bacillary layer, four cells in a circumference and basophilic globules like *Plectus* while *Camacolaimus* has around 256 cells (low polycytous), a rounded lumen, low bacillary layer, six cells in a circumference and reddish-brown non-staining granules.

*Sabatieria* and *Dorylaimopsis*, of the Comesomatidae, are polycytous, having 256 to 500 intestinal cells, six to eight in a circumference, they also have a flattened lumen, a low bacillary layer and large basophilic globules. They differ from one another in that *Sabatieria* is apparently homocytous while *Dorylaimopsis* is heterocytous having scattered cells containing large acidophilic masses (Fig. 104G).

In the Axonolaimidae the intestine is approximately as in the Comesomatidae, there being around 256 cells, six in circumference, a rounded to flat lumen and reddish-brown, non-staining, sphaeroids. Like *Sabatieria*, *Axonolaimus* appears to be homocytous.

In the Monhysteridae there are two quite different types of intestine. In the first, exemplified by *Monhystera* and *Theristus*, the lumen is multiradiate (Fig. 104C') though there are, respectively, 60 and 120 cells, two and four in circumference; the bacillary layer is low and compact and the intestinal inclusions are brownish or grey and basophilic. In the second, exemplified by *Halanonchus*, there are about 566 cells, six to 16 in a circumference; the bacillary layer is relatively higher, less compact, the lumen irregular, and the sphaeroids are brownish and non-staining.

Linhomocids commonly have few intestinal cells in a circumference, usually two in the mid-region of the intestine, but the total number of cells varies considerably. *Tripylium* has 26 cells while *Terschellingia* and *Desmolaimus* exhibit around 128; the lumen is flat to rounded, the bacillary layer low, compact (not resolvable in *Tripylium* but so in the other two examples); the colorless globules in *Tripylium* are soluble in alcohol (therefore presumably fatty), while in *Terschellingia* and *Desmolaimus* the cell inclusions are sphaeroids, slightly brownish, and insoluble.

Unlike other monhysterids and linhomocids, the siphonolaim

intestine is deep red to black in color, the pigmentation being due to refractive, insoluble sphaeroids. Zur Strassen (1904) found the intestine of *Siphonolaimus weismanni* to consist of 22 cells in circumference and to be composed of a total of 6,000 cells (estimation from statements in description); its lumen is rounded, the bacillary layer unusually high.

Members of the Chromadoridae, Microlaimidae and Desmodoridae fall within the lower limits of polycyty, varying within the narrow range of 128 to 256 cells. Seemingly all have a four cell circumference in the mid-region though there may be six to eight in a circumference in the ventricular region. Members of these families have a very low bacillary layer and a rounded to subpolygonal lumen; a moderate number of somewhat basophilic sphaeroids is usually present and in addition, from the coarse vacuolate appearance of the cytoplasm, one might suspect a considerable amount of fatty substances. These three families appear to be homocytous and isocytous.

Members of the Cyatholaimidae, on the contrary, are more distinctly polycytous, varying in cell number from around 256 to 1,000 with from three to 12 cells in circumference; they appear to be uniformly heterocytous. In *Halichoanolaimus* the normal cells contain brown sphaeroids (often appearing in section as basophilic shells) while the scattered heterocytes are devoid of these bodies but contain instead, large vacuoles packed with basophilic globules. In *Synonchiella* the normal cells are vacuolate, without sphaeroids, and the heterocytes are dense, filled with basophilic globules (Fig. 104A). The similarity of the intestine of *Halichoanolaimus* to that of *Dorylaimopsis* is very striking.

Schepotieff (1908) described the intestine of *Desmoscoler* as consisting of few cells and as containing very large brownish globules which were insoluble in alcohol-xytol.

*Enoplida* (Figs. 105-107). The order Enoplida, containing both simple and complex free-living forms, as well as diverse types of parasites, shows extreme variation in the form of the intestine.

Within the Tripyloidea, Stefanski (1916) studied the cell inclusions of *Ironus* and Cobb (1917, 1918) described the intestine of *Ironus* and *Mononchus*. *Ironus* is polycytous and heterocytous (Fig. 106), the number of heterocytes apparently varying with the species. The ordinary cells contain yellowish non-staining sphaeroids which appear as shells with irregular contents in formalin-preserved material. These sphaeroids are sometimes eliminated through the anus (Fig. 105O). *Tripyla* (Fig. 105A-C) is homocytous and barely polycytous, having 136 to 150 intestinal cells, a low bacillary layer, acidophilic granules and scattered polygonal crystals. *Prionchulus* is likewise polycytous and homocytous (Fig. 105D-E); the species differ in having from 170 to 500 intestinal cells; anteriorly the cells in a circumference are more numerous, higher, and have a much more pronounced bacillary layer than in the mid-region but no definite ventriculus is present. Like *Ironus*, *Prionchulus* has acidophilic granules but crystals are absent.

In the Enoploidea Türk (1903), Jägerskiöld (1901), and de Man (1904) studied the intestine of *Thoracostoma* and *Cylcolaimus* and Rantner (1907) that of *Enoplus*; Cobb (1922, 1924a) investigated the intestine of *Eurystomina* and *Anticomma* and Chitwood (1931) that of *Mctoncholaimus*. So far as known, all members of this group are markedly polycytous, isocytous, and have uninucleate cells. With the exception of *Enoplus* they are all heterocytous and even in this form cells are occasionally found which differ from their neighbors in the presence of large acidophilic bodies. Türk found the homocytes of *Thoracostoma* to contain greenish-brown granules. Specimens kept in clean white sand had a clear intestine free from such inclusions. He judged these inclusions to be resorption vacuoles of plant food. Occasional heterocytes he interpreted as fat cells (Fig. 105M-N). A bacillary layer appears to be totally absent in *Mctoncholaimus*, *Thoracostoma* and *Cylcolaimus*. This layer is represented merely by a peripheral condensation in *Eurystomina* (Fig. 105G-II) and *Leptosomatum* (Fig. 105L) while it is moderately high and distinct in *Enoplus* and very high, especially in the ventricular region, of *Phanodermopsis*. The ordinary cells (homocytes) of *Phanodermopsis* contain yellowish non-staining sphaeroid shells (Fig. 105I) while the corresponding cells of *Leptosomatum* have a conspicuously vacuolate plasma (? fat vacuoles) and a few basophilic globules; the homocytes of the remaining forms contain acidophilic granules. Heterocytes in *Eurystomina* and *Phanodermopsis* are filled with basophilic globules while the heterocytes of *Leptosomatum* include a large amorphous acidophilic vacuole and those of *Mctoncholaimus* may either be basophilic with a large vacuole or contain scattered large yellowish non-staining sphaeroids (Fig. 105F). Chitwood and Chitwood (1938) identified fats and ferrous



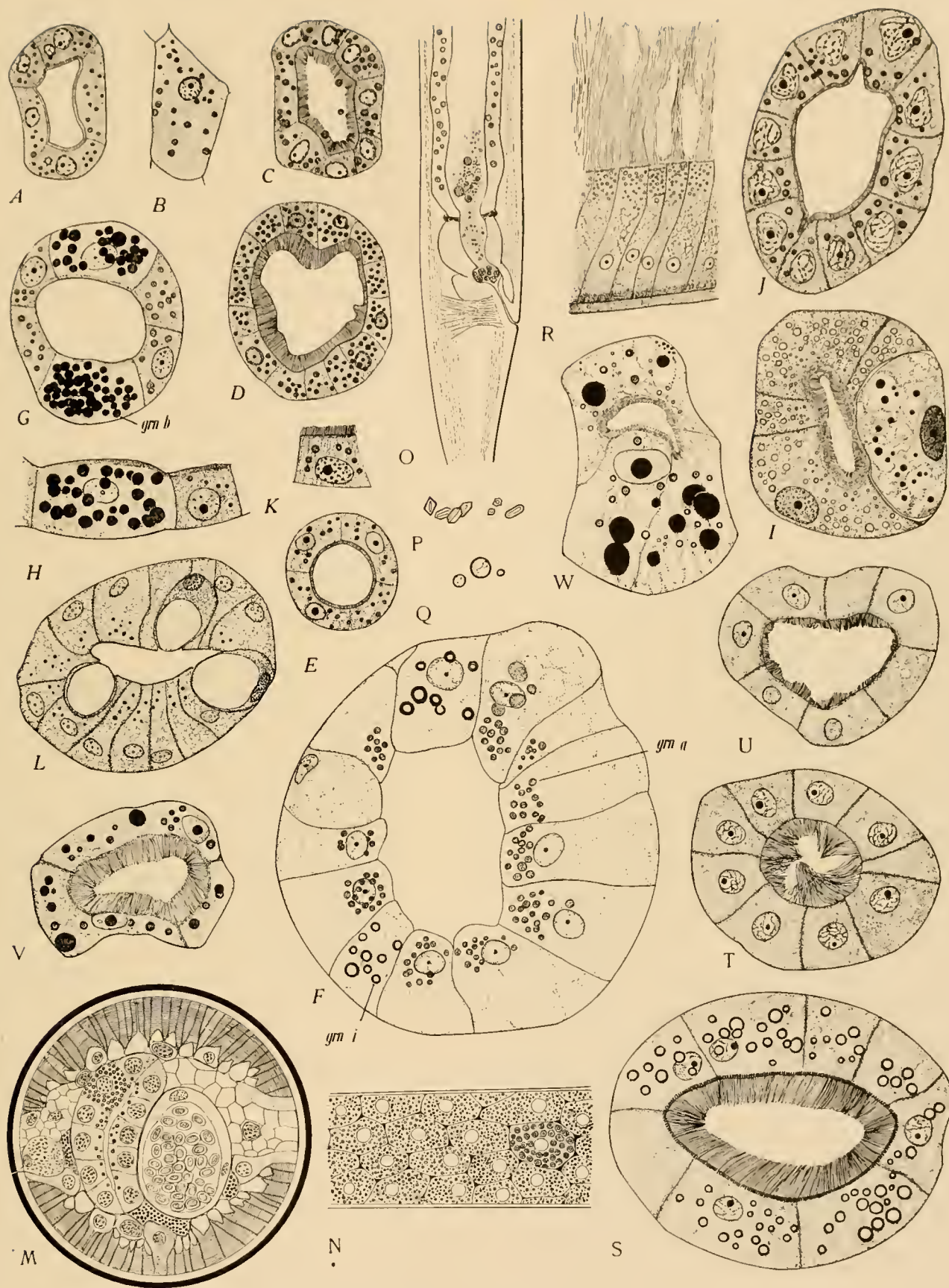


FIG. 105. INTESTINE IN ENOPLIDA

A-C—*Tripyla papillata* (A—posterior part; B—surface view; C—ventricular region). D-E—*Prionchulus muscorum* (D—ventricular region; E—mid-region). F—*Metoncholaimus pristiurus*. G-H—*Eucystomina americana*. I—*Phanodermopsis longisetus*. J-K—*Enoplus communis* v. *meridionalis* (J—mid-region; K—ventricular region). L—*Leptosomatum elongatum* v. *acrophalatum*. M-N—*Thoracostoma strasseni*. O-Q—*Iranus tenuicaudatus* (O—

note sphaeroids in rectum; P—isolated crystals; Q—isolated degenerate sphaeroid shells). R—*Diectophyma renale*. S-U—*Dorylaimus stagnalis* (S—mid region; T—posterior part of prerectum; U—prerectum). V-W—*Leptanchous* sp. (V—ventricular region; W—mid-region). M-N, after Tuerk, 1903, Mitt. Zool. Stat. Neapel, v 16; remainder original.



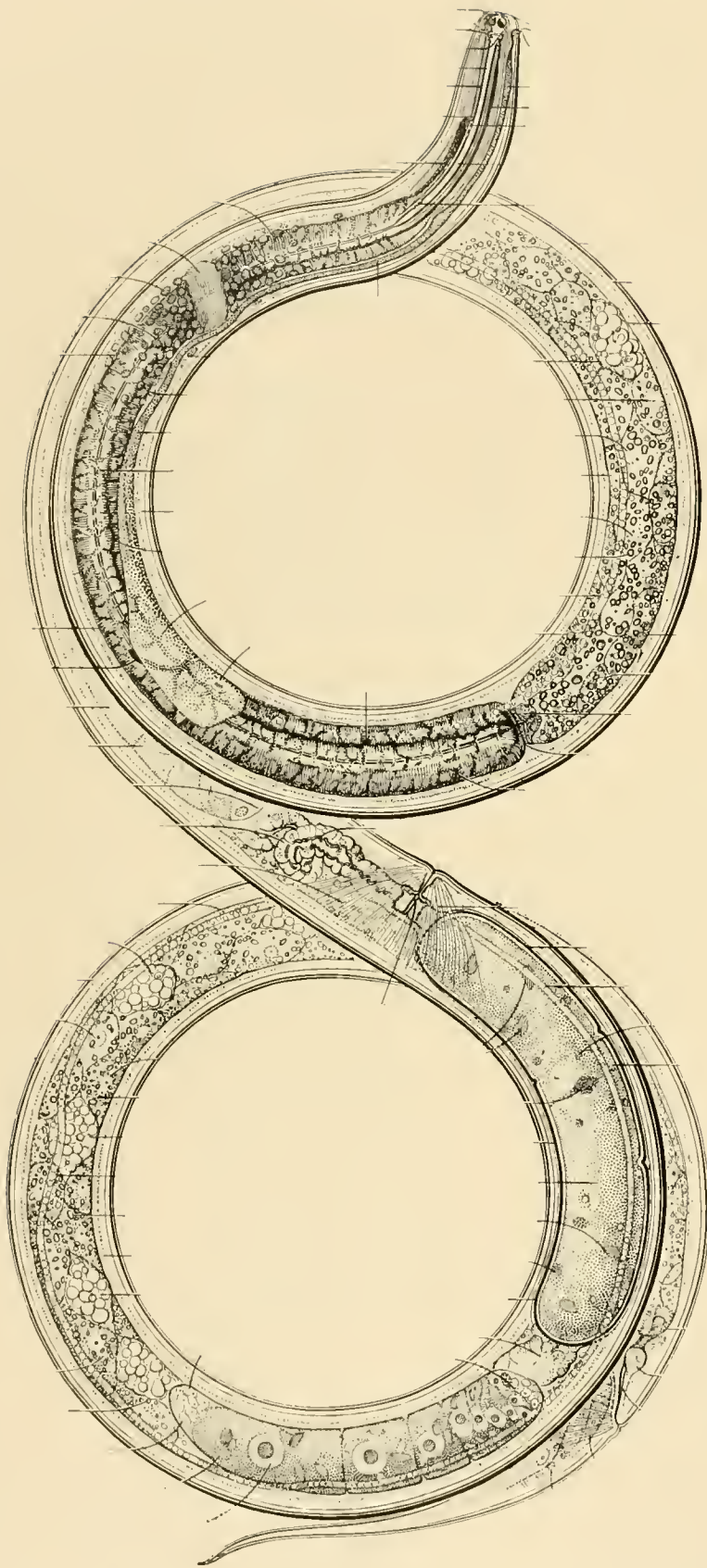


FIG. 106

*Ironus tenuicaudatus*. (Note specialized intestinal cells containing large globules, also small polyhedral crystals in ordinary intestinal cells). After Cobb, 1918, Contrib. Sc. Nemat. 7.

iron salts as the chief cell inclusions of an oncholaimid.

The number of dorylaimoids of which the intestine has been studied is inadequate. Members of the Dorylaimidae all seem to be polyeyctous but the number of cells in an intestinal circumference varies from four to 20. Anteriorly the bacillary layer is highest in the ventricular region and posteriorly a conspicuous change is notable in this layer in the prerectum. Throughout ventricular and mid-regions the cells contain yellowish brown non-staining sphaeroids (appearing as shells in section) while these structures are absent in the prerectum. The latter is set off as a distinct section of the intestine in the Dorylaimidae (Figs. 20-21) and Leptonchidae and may even be subdivided into two distinct units in *Actinolaimus*. *Leptonchus* resembles dorylaimids in general but differs in that the number of intestinal cells is smaller (oligocytous) and the cells contain massive basophilic globules. Nothing is known concerning the intestine of the diptherophorids aside from the fact that they have no prerectum.

The intestine of the Mermithoidea has been given more attention than that of other groups because, as was early recognized, the peculiar nature of the intestine constitutes one of the major characteristics of the group. Schneider (1860) first recognized that the solid mass of tissue which Meissner (1853) called the "Fettkörper" corresponds to the mesenteron of other nematodes. The work of Meissner (1853, 1856), Schneider (1860), Rauther (1906, 1909), Hagmeier (1912), Steiner (1933), and Christie (1936) makes it possible to characterize the mermithid intestine as an organ of food storage in which the larva, during the parasitic stage, stores the nutrient matter on which it draws throughout adult life and reproduction. In order to meet these requirements the intestine grows anterior to the base of the esophagus, regularly reaching the level of the nerve ring. Rauther (1909) observed a lumen (Fig. 107F) in the anterior part of the intestine of *Mermis* sp. and interpreted this part of the intestine as a caecum. Steiner (1933) stated that in some mermithids the trophosome has an axial cavity and a wall of polynucleate cells, while in others the axial cavity disappears but the polynucleate cellular condition persists, and in still others the cell walls disappear forming a synectium. Rauther found that the intestine of *Hezarmermis albicans* consists of two longitudinal rows of cells each containing 10 to 15 nuclei in the adult stage while the writers found the intestine of *Agamermis decaudata* (Figs. 107A-C) to be four to 10 cells in circumference and each cell to contain 22 to 25 nuclei. The total number of cells in these forms appears to fall within the upper limits of polycycty. In *Hydromermis* sp. the nuclei are relatively larger (Fig. 107E) and apparently less numerous than in the previously mentioned forms but unfortunately no exact information is available. Large vacuoles containing crystals or crystal aggregates have been observed in several mermithids in all stages from the preparasitic larva to the senile adult; these crystals accumulate with age, becoming a conspicuous feature of specimens after reproduction has ceased. The increase in crystals and vacuoles coincides with diminution of intestinal globules. Rauther (1906) compared the crystals with uric acid but was unable to obtain an unmistakable murexide reaction. Concerning the globules of nutritive reserve, the following observations have been made on *Agamermis decaudata*: Sections of young parasitic larvae contain only a few basophilic globules in a rather dense cytoplasm (Fig. 107B); the larvae at emergence and the young adults are literally packed with such globules in a vacuolate cytoplasm; the cells of specimens in the emerging larvae and adults are filled with colorless, oily appearing globules (whence the name fat body); according to Chitwood and Jacobs (1937) only a small proportion of these globules is fat, the great majority being protein.

The superfamily Trichuroidea is typically myriocytous, anisocytous, homocytous and the intestinal cells are uninucleate. Villus formation in *Trichuris* is uniform, the subpolygonal units (groups of cells) causing much the same appearance as large individual cells in surface view; from this standpoint there is distinct parallelism with *Oxyuris* (Fig. 103E). Actually each unit is composed of 50 to 100 tall narrow cells. The bacillary layer is quite high in the mid-region and the basal layer is unusually thick. Reddish-brown sphaero-crystals are present throughout the mid-region of the intestine.

The intestine of the dioctophymoids is much like that of the trichuroids, differing only in that the bacillary layer (Fig. 105R) may reach a height nearly equal to that of the cell proper. The sphaero-crystals are localized on the side toward the lumen and villi are not uniform.



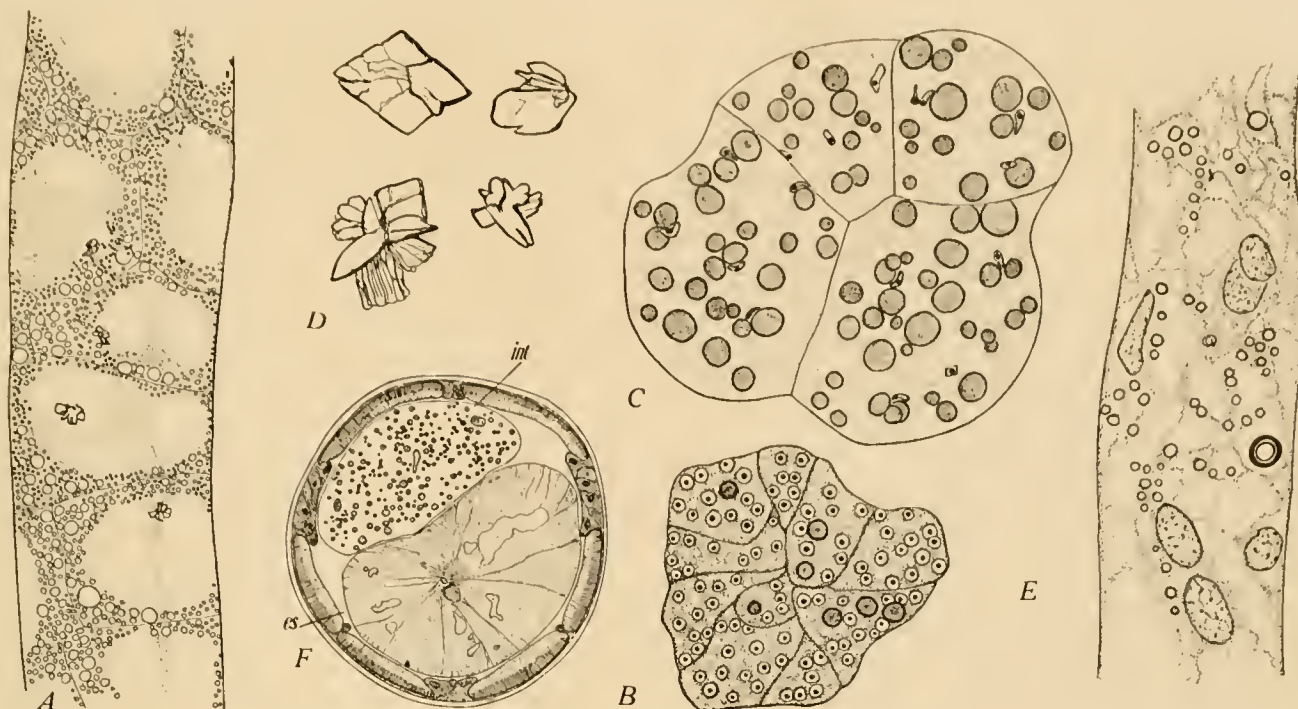


FIG. 107

Intestine of mermithoids. A-D—*Agamermis decaudata* (A—trophosome of senile male, dissected alive; note remnants of protoplasm near edge of cells and large vacuoles; B—Cross section of large larva (1 cm) from body cavity of grasshopper showing dense protoplasm, at times protein globules [shaded] begin to appear, nuclei circles with

central nucleolus; C—Cross section of adult, non-senile showing numerous protein globules, note relatively minute nuclei; D—Crystals as seen in A). E—*Hydromermis* sp. (longitudinal section of adult). F—Cross section of entire *Mermis* sp. showing intestine with lumen. A-E, original; F, after Rautner, 1909, *Ergeb. u. Fortsch. Zool.* v. 1(3).

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# CHAPTER VIII

## THE POSTERIOR GUT

### (STRUCTURES OF THE PROCTODEUM)

The existence of a complete digestive tract terminated by an anus and of separate sexes was discovered by Tyson (1683) in *Ascaris*; he probably observed the spicules also but was unable to interpret them correctly. Soon afterwards it was established that the intestine of the female connects by means of a valve or sphincter with the posterior gut (rectum) and thence with the outside through a ventrally situated anus. With one exception, the female reproductive system never connects with the rectum; in the genus *Rondonia Travassos*, 1920 (Atractidae) the vagina joins the rectum (Fig. 108L) to form a cloaca. This condition is approached in several other forms particularly *Aorurus agile* (= *A. subeloatus* Christie, 1931, Thelastomatidae) and *Eustrongylides tricolor* Sugimoto, 1931 (Dioctophymatidae) but an internal junction of vagina and cloaca exists only in *Rondonia*. In the male, the reproductive system always joins the rectum, forming a cloaca from the walls of which various copulatory structures develop. Since there is usually a definitely elongate tail, the anus or cloacal opening is ventral. In exceptional groups characterized by the absence of a tail, such as the Trichuroidea and Dioctophymatoidea and in scattered representatives of other groups the anus or cloacal opening may be terminal or subterminal. Male strongylins can hardly be placed in this category since the dorsal ray represents the tail and the *genital cone* is developmentally a ventral outgrowth of the cloacal lips. The intestino-rectal valve, cloaca, spicules, gubernaculum and telamon are all included under the general heading of posterior gut since, with the exception of the intestino-rectal valve, they are wholly formations of the proctodeum. The valve is quite diverse, formed sometimes chiefly, sometimes entirely from endodermal tissue, but in all instances it functions as a part of the rectum. Other structures are essentially modifications of the rectum and will be discussed from that standpoint.

#### A. RECTUM, INTESTINO-RECTAL VALVE AND RECTAL GLANDS

The rectum is a more or less flattened, subtriangular or irregular tube lined internally by a cuticular layer underneath which there is a layer of large epithelial cells, and covered externally by mesenteric and muscle tissue. Leuckart (1876) was under the impression that the cuticular layer of the rectum was continuous not only with the external cuticle but also with the bacillary layer of the intestine. Voltzenlogel (1902) found Leuckart to be in error regarding the latter connection. The cuticular lining of the rectum ends slightly posterior to the junction of mesenteron and proctodenum leaving the rectum naked for a short distance. Though Voltzenlogel made this observation on *Ascaris* it was confirmed by Martini (1916) for *Oxyuris* and the writers for such diverse forms as *Mecyncholaimus*, *Cephalobellus*, *Dioctophyma* and *Trichuris* (Oncholaimidae, Thelastomatidae, Dioctophymatidae, and Trichuridae, respectively). All investigators have found the rectal cuticle to be continuous with the external cuticle. It is known to be cast off at the molt with the remainder of the exuvium. Voltzenlogel and Martini both observed that the fiber layers and striation of the external cuticle cease at the inner side of the anal lips; farther inward the rectal lining consists of cortical, matrix and basal layers (see p. 30). However, there is considerable thickening of the first two layers in most parasitic nemas.

It is impractical to discuss the rectal epithelium without first considering the rectal glands since there has been much confusion in interpretation. Walter (1856) was supposed by Bastian (1866) to have first seen the large cells at the junction of the intestine and rectum in *Cosmocerca trispinosa* (*Oxyuris ornata*) and to have mislabeled them nerve cells. Actually Walter was entirely correct; the structures he illustrated were the paired preanal ventral ganglia. Shortly thereafter Claparede illustrated the cells now known as rectal glands in "*Ascaris commutata*" and "*A. mucronata*" labeling them anal glands. Since that time similar structures have been reported from many parasitic nematodes. Eberth (1860, 1863) illustrated "anal glands" in *Heterakis vesicularis*, *Draschia megastoma*, and *Passalurus ambiguus*; Macalister (1865) mentioned them in *Atractis daetylara* and was the first to suggest

that they might be homologues of the malpighian tubules of insects; Bastian (1865) described anal glands in *Anticomma* spp., *Linkomocus*, *Halichoanolaemus*, and *Cyatholaemus*; Butschli (1873) described anal glands in *Rhabditis aspera*; Leuckart (1876) mentioned six anal glands in *Ancylostoma*; de Man (1886) described various cells around the rectum in *Enoplus*, *Oncholaimus*, and *Anticomma* as anal glands; Hesse (1892) working on *Parascaris* interpreted the large cells as "Gewebebolster" cells; Augstein (1894) observed anal glands in *Dictyocaulus filaria*; Shipley (1894) described anal glands in *Toxascaris transfuga* but later (1897) presumed them to be identical with the giant "büschelförmige Organe" (Coelomocytes, see p. 45); Jägerskiöld (1893, 1894) described anal glands and a unicellular sphincter muscle in *Contracacuum claratum*; Hamann (1895) gave a very good description of both rectal glands and rectal epithelium in *Goczia* (Anisakinae); Ehlers (1899) and Jerke (1901) mentioned rectal glands in *Oxyuris equi*; Looss (1901) described cells forming a "rectal ligament" in members of the Strongylidae considering the whole group of cells in this region as being non-glandular; Voltzenlogel (1902) gave an excellent description of the rectal glands, rectal epithelium, etc., of *Ascaris*; Looss (1905) denied the existence of rectal glands in *Ancylostoma* and interpreted these cells as part of a "rectal ligament" which view was concurred in by Immek (1924) working on *Strongylus*. Törnquist (1931) working on *Cueullanus* and *Camallanus* and Mackin (1936) studying *Spironoura*; Martini (1916) published thorough descriptions of the rectal glands, epithelium and musculature of *Oxyuris*; finally Magath (1919) considered the rectal glands as sarcoplasm of the sphincter muscle.

Controversy over the function of cells of the rectal region has confused the picture, especially since some workers deny the existence of functional glands opening into the rectum. Recently the writers (1930, 1931, 1933) observed the orifices of such glands into the rectum in *Rhabditis*, *Heterakis*, *Maeracis*, *Cephalobellus*, and *Hystrignathus* (Rhabditidae, Heterakidae, Oxyuridae and Thelastomatidae respectively) and similar gland orifices were reported by Baker (1936) for *Heterakis*. It does not, however, necessarily follow that all of the structures in the past termed glands are homologous with the structures described by the above mentioned authors. As will be seen later, rectal glands are by no means a universal feature in nematodes. However, it is considered certain that the structures described by Jägerskiöld, Hamann, Voltzenlogel and Martini are rectal glands.

Hamann reports that the rectal epithelium of *Goczia* is composed of two pairs of cells, one pair anterior and one pair posterior to the rectal glands (Fig. 108J). In *Ascaris*, Voltzenlogel found four large epithelial cells forming an anterior circle (Fig. 108I) and additional cells posterior to them but the latter were not constant in position. In *Oxyuris* Martini describes the rectal epithelium as composed of seven cells, an anterior ring of three, (one dorsal and two subventral) and two pairs of cells arranged in tandem posterior to the first group (Fig. 109W-X). In females of *Goczia*, *Ascaris*, and *Oxyuris* there are three rectal glands projecting into the body cavity and having processes which penetrate the rectal epithelium. Voltzenlogel was the first to show that there is sexual dimorphism in the number of rectal glands; he reported six rectal glands for male ascarids; Martini later found the same number in males of *Oxyuris*.

Confusion in regard to the structures has been due to two factors; the rectal glands may be embedded in the lateral and dorsal chords or they may be associated with the vas deferens. Thus Mackin described the rectum of *Spironoura* as composed of 10 cells in the female, three forming a "rectal ligament," and 14 in the male, two in a dorsal "ligament," two in a "genital ligament," and one in each of two ligaments extending to the lateral chords. All of the cells designated "ligament cells" by Mackin are rectal glands; those of the "genital ligament" are embedded in the wall of the vas deferens but have separate orifices into the rectum (Fig. 110MM). The "small ejaculatory glands" described by Chitwood (1930, 1931) in *Rhabditis* (Fig. 3, ej 2) *Maeracis* and *Heterakis* and



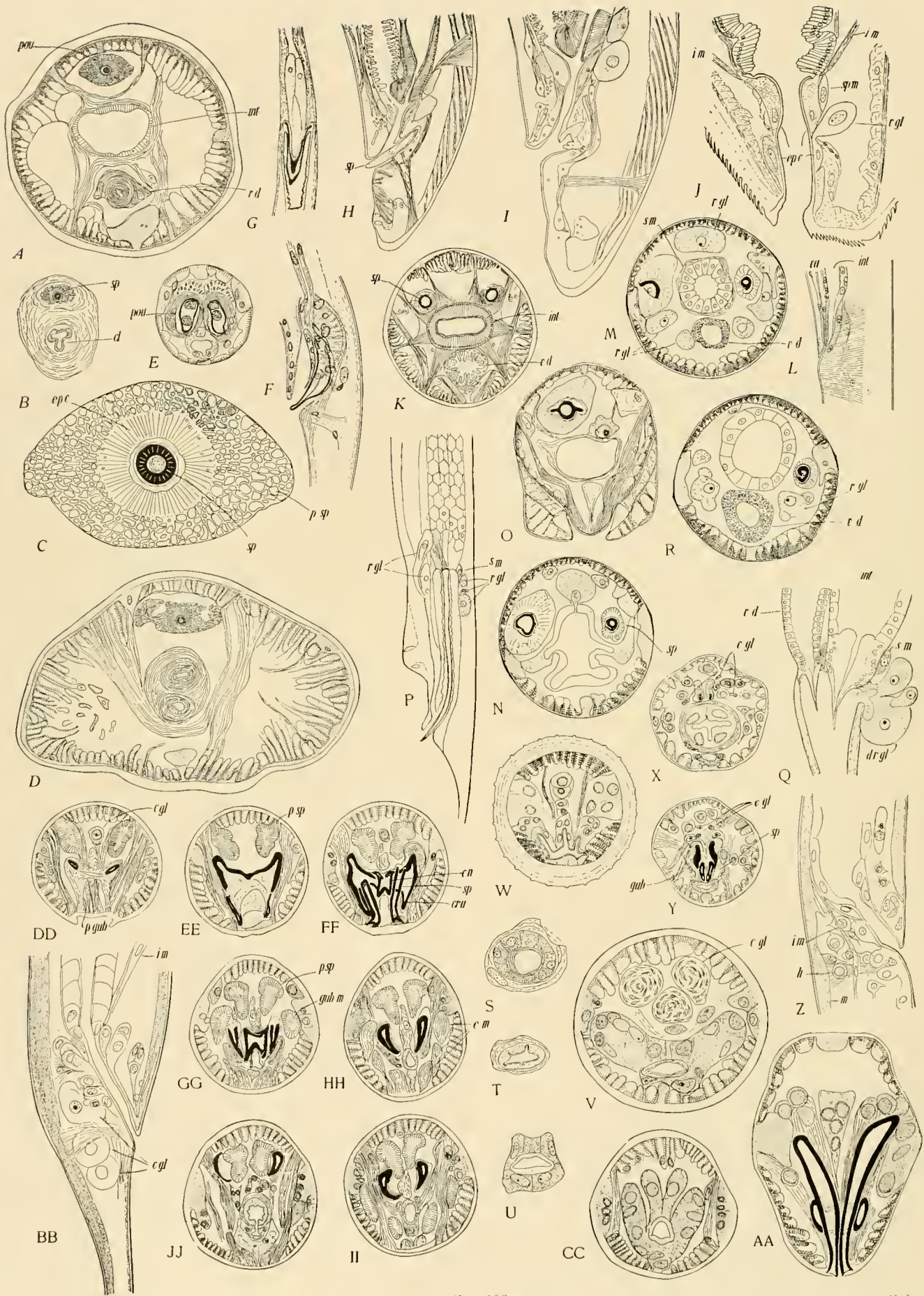


FIG. 108  
A-D—*Diocetophyma renale* (A—Cross section through posterior part of male showing spicular pouch, intestine and vas deferens; B—Cross section through cloaca and spicule near its entrance into cloaca; C—Cross section of spicular pouch showing cuticular lining, cloaca; and protractor muscle; D—Cross section more posterior to A near junction of rectum and vas deferens). E-F—*Trippyla*



by Baker (1936) in *Heterakis*\* are also rectal glands and correspond to the cells of the "genital ligament" described by Mackin.

From these observations, it appears that three rectal glands in the female and six in the male is the rule for members of the Rhabditoidea and Ascaridina and for at least some members of the Spiruroidea. However, rectal glands appear to be totally absent in the Tylenchoidea. The rectal ligament cells described by Looss and Imminck for strongyloids are in part rectal glands. Such glands occur in representatives of all suborders of the Phasmidia but appear to be absent in a few isolated types and groups such as *Dracunculus*, *Diroflaria* and tylenchoids. Perhaps the absence of rectal glands in these forms will be explained in the future on physiological grounds when their function becomes known.

In the Aphasmidia no single case has thus far been definitely established of the existence of rectal glands. Though mentioned by Eberth (1863), Bastian (1865) and de Man (1886) it is notable that no later mention was made of such glands by de Man (1904) nor by Jägerskiöld (1901). The best substantiated record of such occurrence is in *Enoplus communis* as illustrated by de Man (1886). The writers have been able to identify the numerous cells shown by that author as attached to the rectum but all appear to be separated from the rectal lumen by the cuticular rectal lining (Fig. 108 BB). This is in sharp contrast to the established cases such as *Spironoura* and *Heterakis* (Fig. 108N, 110 Y & MM) in which there is a distinct break in the cuticle at the level of each gland orifice. It is concluded that in *Enoplus communis* the cells in question are merely epithelial cells. Careful study of *Cylicolaimus* and *Thoracostoma* by Jägerskiöld (1901) and Türk (1903), of *Trichuris* by Rauter (1909, 1918), of *Metoncholaimus*, *Leptosomatium*, *Tripylla*, *Prionchulus*, *Diectophyma*, *Sobolipyme*, *Aphanolaimus*, *Halichoanulaimus*, *Paracanthochus* and *Dorylaimopsis* by the writers failed to reveal rectal glands in a single case. In *Anaplectus granulosus*, female totomount specimens appear to show three rectal glands but we have not been able to verify the point in sections. Pending further proof it is concluded that aphasmidians are usually without rectal glands. In the male of *Dorylaimus prolificus* (Fig. 21) there is a group of four pairs of cells near the anterior end of the prerectum which appear to be glandular; in living specimens one may trace a slender tube leading from each cell posteriad nearly to the intestino-rectal valve where each tube

turns ventrad and disappears between the vas deferens and the intestine; the homologues of the above mentioned cells are not known.

The intestino-rectal valve is a very simple structure, consisting, in oligoeytous forms such as *Rhabditis*, of the posterior parts of the prerectal intestinal cells surrounded by a sphincter muscle. In polyeytous and myrioeytous nematodes the intestinal cells in the valve region become much smaller, more numerous, and are often devoid of a bacillary layer. They may form a valve either by reflexure into the intestinal lumen or extension into the rectal lumen (Fig. 108Q & 109W).

The musculature controlling the intestino-rectal valve, rectum, and anus has already been briefly discussed (p. 43). The existence of a uninnervate sphincter muscle was first made known by Jägerskiöld (1893, 1894) and Gilson and Pantel (1894). Later workers have often confused other structures with the sphincter and described sphincter muscles with two, four or more nuclei (Magath, 1919, in *Camallanus*, and Chitwood, 1931, in *Macracis*). Reexamination of representatives of all groups of the Nematoda by the writers establishes the unicellular sphincter as universally present. It is a circular band of fibers containing a single nucleus which may be dorsal, ventral, or lateral in position. Its innervation process extends anteriorly to the dorsal nerve in *Ascaris* according to Voltzenlogel. This muscle closes the intestino-rectal valve preventing reentry of materials from the rectum into the intestine during defecation.

The depressor ani, an U-shaped muscle, is likewise unicellular and of universal occurrence. It is this muscle that elevates the dorsal wall of the rectum causing materials to be drawn into the rectal cavity; it then elevates the posterior lip of the anus thus permitting defecation. The rectum is devoid of circular muscles and for the most part defecation is accomplished by pressure. Subventral and subdorsal somato-intestinal muscles (Fig. 52) probably supply the pressure by dilating the prerectal lumen, thus drawing materials into that region from the mid-region of the intestine and forcing them into the rectum by relaxing at the same time that the rectal sphincter relaxes and the anterior part of the depressor ani contracts; by such means the rectal cavity is filled. Thereafter the rectal sphincter contracts, the anterior part of the depressor ani relaxes and the posterior part contracts; pressure on the walls of the distended rectum by the body fluid causes it to collapse and the waste products to be forced out.

## B. CLOACA

The vas deferens enters the rectum from the ventral side in males of all groups with the sole exception of the Trichuroidea. In trichuroids Rauter (1909, 1918) found that the vas deferens enters the rectum dorsolaterally (Fig. 110 Z-DD). In phasmidians the junction of vas deferens with hind gut is nearly simultaneous with or immediately posterior to the intestino-rectal valve so that practically no rectum exists; the whole of the hind gut is then transformed into cloaca. In some aphasmidians, particularly enoploids, the vas deferens is apt to join the rectum somewhat more posteriad so that both a rectum and a cloaca may coexist.

## C. SPICULAR POUCH

With few exceptions, which will be discussed later, the spicules enter the cloaca from the dorsal side immediately anterior to the anus. They develop in a pair of cell masses, the spicular primordia, which develop as proliferations of the dorsal wall of the cloaca, first described correctly by Seurat (1920) in *Falcaustra lambdiensis* (Fig. 110 OO). Schneider assumed the presence of a single primordium in nematodes with two spicules but this is incorrect. Previous to the formation of the spicules the primordia are without a lumen, as may be seen in *Enoplus* (Fig. 108 CC), but later developmental phases indicate that the spicular primordia should be interpreted as instances of suppressed evagination followed by terminal invagination. The primordia become differentiated in such a manner that they form a pouch which contains the spicules. As shown by Voltzenlogel (1902) the pouch is lined with a cuticle continuous with that of the cloaca. It is covered by an epithelium which is also continuous with that of the cloaca. When two spicules are present, the paired spicular pouches always join before entering the cloaca. In parasitic nematodes this pouch and the protractor muscles of the spicules form an obvious spicular covering termed the sheath. In free-living nematodes the spicular pouch is often extremely delicate\* and easily overlooked. Possibly for this reason Türk (1903) denied the existence of a pouch in *Thoracostoma* where it had been previously observed and illustrated by Jägerskiöld (1901).

\*The pouch wall and cuticle were inadvertently omitted in Fig. 49 E, L, M. They are delicate but nevertheless present in this form.

\*In *Heterakis gallinae* one finds six additional smaller cells in the body cavity, a dorsal pair, one situated on each side of and between the large pair of tandem dorsal rectal glands (Fig. 108, N, P), and two subventral pairs, one situated on each side of each of the large ventral rectal glands (Fig. 108 P, R). These cells seem to have ducts into the cells to which they are attached. They may conceivably be subsidiary rectal glands. Increase in rectal gland number from three to six and possibly to 12 seems to support the view of Macalister that they are homologues of the malpighian tubules of insects. Martini (1913) aptly indicated the unicellular rectal glands of nematodes as precursors of the groups of unicellular glands of *Macrobolus* which in turn are undoubtedly forerunners of the multicellular tubular glands of other tardigrades. These last mentioned are, in turn, considered as identical with the malpighian tubules of insects. This view, though questioned by Seurat (1920) seems logical in view of the fact that multicellular tubular glands normally, in evolution, arise by reduplication of associated unicellular glands with common acini.

*papillata* (E—Cross section of male in region of cloaca and spicular pouches; F—Longitudinal section in same region). G—*Parascaris equorum* (Longitudinal section through proximal end of spicule showing spicular cells). H—*Ascaris lumbricoides* (Longitudinal section through caudal region of male). I—*Parascaris equorum* (Longitudinal section through caudal region of male). J—*Goezia annulata* (Longitudinal section through caudal region of female). K—*Parascaris equorum* (Cross section of male anterior to intestino-rectal valve). L—*Rondonia rondoni* (Lateral view showing vagina opening into rectum). M—*Heterakis gallinae* (All illustrations of male). N—At level of intestino-rectal valve; O—At level of rectal gland orifices; P—At level of preanal sucker; Q—Reconstruction of cloacal region; Longitudinal section at intestino-rectal valve showing, sphincter muscle, double dorsal gland and secondary dorsal gland; R—Cross section considerably anterior to intestino-rectal valve showing paired subventral glands and their accompanying cells, secondary glands). S—*Leptosomatium elongatum* v. *acephalum* (S—Intestino-rectal valve, inner cells are intestinal; T—Section following S; U—Rectum showing epithelial cells; V—Preadult male showing spicular primordia). W—*Dorylaimus stagnalis* (Cross section showing rectum of female). X—*Metoncholaimus pristiurus* (X—Cross section of male at level of intestino-rectal valve; Y—Cross section of cloacal region of male showing spicules and gubernaculum; Z—Longitudinal section of female: there is no evidence of rectal glands or a break in the rectal cuticle such as one would expect in that case). AA—*Eurytomina americana* (Cross section of male at cloacal opening). BB—*Enoplus communis* v. *meridionalis* (BB—Longitudinal section of female in rectal region, as in Z, there is no evidence of rectal glands; CC—Cross section of preadult male showing primordia of spicules and gubernaculum crura; DD—Serial sections through cloacal region of male, beginning postanal and going anteriorly, some sections omitted between most anterior sections). G-I & K, after Voltzenlogel, 1902, Zool. Jahrb., Abt. Anat., v. 16; J, after Hamaon, 1895, Die Nematelminthen v. 2; L, after Baylis, 1936, Ann. & Nat. Hist. s. 10, v. 17; remainder original.



FIG. 109  
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It has been seen in all free-living nematodes studied by the writers. The protractor muscles of the spicules form a complete longitudinal muscle layer on the surface of the pouch in most parasitic nematodes but in free-living nematodes these muscles are more commonly confined to the dorsolateral sides. The pouch and accompanying muscles are most conspicuous in *Tripyla* and *Triplonchium* of the free-living nematodes and give an appearance (Fig. 108F) which is peculiar to these genera and their relatives. In the Strongylini and Dioctophymatini the spicular pouch commonly joins the cloaca some distance anterior to the anus and in the Trichuroidea this tendency is carried to an extreme (Fig. 110 DD). In other groups of nematodes the spicules can scarcely ever be said to lie within the cloaca even for a short distance; actually they merely pass through a common cloaco-spicular orifice. Mueller (1925) and Chitwood and Chitwood (1933) found the spicules of *Proleptus* and *Cephalobellus* to have a separate aperture immediately posterior to the cloacal opening.

The spicular pouch should under no circumstances be confused with the so-called spicular sheath of *Trichuris*, which was named the *cirrus* by Rauter (1909). It is a unique occurrence in the Nematoda that in *Trichuris* and relatives the lining of the cloaca (cirrus) is itself evertible and often armed with teeth (Fig. 109L); this structure is capable of being inserted with the spicule into the vagina during copulation and undoubtedly serves as a true penis. It is in direct continuity with the external cuticle and when retracted there are three layers (Fig. 110 AA) of cloacal lining. The feces must pass through the cirrus for evacuation to take place.

#### D. SPICULES

Nematodes usually have two spicules, each spicule being essentially a tube covered by a sclerotized cuticle and containing a central protoplasmic core. Its cuticular covering is continuous with the cuticular lining of the spicular pouch and from that standpoint the spicules may be regarded as evaginations of the spicular pouch. The cuticle is often layered, the outer layer (Fig. 109 CC) being colorless and structureless while the inner layer or layers are tan to brownish and sometimes are composed of numerous prismoidal elements. In other cases the spicules may appear to be spongy or reticulated (Fig. 110 NN). The prismoidal elements (Fig. 109 CC) should not be confused with the so-called striation such as occurs in *Stenurus* (Fig. 33 K), *Protostrongylus* (Fig. 110 EE), etc. Such striation is due to the extension of the sclerotized ribs into a weak or non-sclerotized flange. The central protoplasmic core of the spicule may or may not contain the nuclei of the spicular epithelium. These cells and nuclei are often situated anterior to the proximal end of the spicules, surrounded by the retractor muscle. Their number is variable, four being recorded in *Ascaris* (Fig. 108 G & K). Ordinarily one finds each spicule provided with two retractor muscles and two protractor muscles. Both pairs of muscles are attached to the proximal end of the spicule. The retractors extend anterior and toward the lateral chord where they may be attached to the body wall either subdorsally, dorsolaterally or ventrolaterally dependent upon the species involved. The protractors tend to surround the spicular sheath and may be inserted postanally to the body wall or to the dorsal side of the spicular pouch. In those groups in which a single spicule is present, the retractor muscles extend to both the right and the left body walls. In exceptional instances the protractors and retractors are composed of numerous cells which form a longitudinal muscle layer on the spicular pouch (Figs. 108 A, C & 110 DD) that is quite characteristic of the groups involved (Trichuroidea and Dioctophymatoidea). As a rule each spicule may be divided into three

sections, the head (capitulum), shaft (catomus), and blade (lamina). The head is the modified portion of the proximal end; the shaft is the tube-like part between the head and the blade; the blade is the distal portion which is usually flanged (Fig. 110 DD-EE). There may be one or two flanges; if one, it is ventral as seen in cross section and if two, one is dorsal and one ventral (Fig. 110 MM). Though such differentiation of the spicule into regions is the rule, no such regions are apparent in *Dioctophyma* or *Trichuris*. Extensive diversity occurs in the spicular form.

Two is the basic number of spicules in nematodes and they originate from a double spicular primordium as stated by Senrat (1920). However a single spicule occurs in many groups of nematodes. It is a characteristic of the Trichuroidea, Dioctophymatoidea, Oxyuridae and Thelastomatidae and also occurs in isolated genera of the Desmodoridae (*Monoposthia*), and Mermithidae (*Hydromermis*). In other groups it is not uncommon for the spicules to be distally fused and stages with nearly complete fusion are known. Thus, in *Rhabditis strongyloides* (Fig. 109 EE, H-J), *R. terricola* (Rhabditidae) and *Nematodirus aspinosus* (Trichostrongylidae) the distal ends of the spicules are fused. In the subfamily Ransomnematinae of the Atractidae, there is a complete series of stages in fusion, including forms such as *Carnoya* with two entirely separate spicules, *Heth* and *Augra* with nearly completely fused spicules, and *Pulchrocephala* with no spicules. In the Mermithidae there is a similar series from *Mermis* with two separate spicules, to *Paramermis elegans* (Fig. 109 D-E) with partially fused spicules, and *Hydromermis* with a single spicule. Genera and species completely devoid of spicules are of sporadic occurrence but usually, if not always, such forms are confined to groups characterized by a tendency toward spicular fusion or presence of a single spicule. Thus we find *Trichinella* of the Trichuroidea, *Aspicularis*, *Dermatoryx* and several but not all species of *Pharyngodon* (all representatives of the Oxyuridae), *Hystriognathus* of the Thelastomatidae and *Pulchrocephala* of the Atractidae characterized by the absence of spicules. There have been two divergent views on the interpretation of unpaired spicules. One group, led by Schneider (1866), maintains that it is a neotenic character resulting from a failure of division of an originally unpaired spicular primordium. As has been previously noted, this view is based on the erroneous assumption that in two-spicule nematodes the spicular primordium is originally single. Other authors have considered the single spicules as resulting from reduction by loss of one spicule. In view of the several series showing spicular fusion, this theory seems hardly tenable. As Cobb (1898) pointed out, the retractor muscles of the single-spicule forms go to both sides of the body wall, indicating the double character of the spicule.

Diversities in spicular morphology are too numerous to be covered completely. The general form is often quite diagnostic, being used as generic and specific characters throughout the Nematoda. Unfortunately the shapes vary so much and are sometimes so complicated that one must rely chiefly on illustrations. Cobb (1898) provided some descriptive terms which might well be more widely applied (Fig. 109 NN). As a rule the spicules of free-living nematodes are equal and similar. In parasitic nematodes, particularly the various groups of the Spiruroidea, Filarioidea, and some species of the Heterakidae, Ceuallanidae, Camallanidae and Atractidae the spicules are unequal and dissimilar. Asymmetry in the form of the spicules is given varying significance in the different groups. Usually the left spicule is longer than the right but in some forms the converse is the case (*Heterakis gallinae*). The blade of the longer spicule is generally alate (Fig. 109 T) and sometimes bears a distal hook. The shorter spicule is usually heavy-

Fig. 109

A-C—*Hyostromylus rubidus* (A—Lateral view of male tail; B—ventral view; C—Detail of telamon, specimen cleared in phenol). D-E—*Mermis elegans* (D—Lateral view of male tail; E—tip of spicules). F—*Tetrameres inermis* (Full length of male, showing greatly elongated left spicule). G—*Ostertagia circumcincta* (Spicules and gubernaculum); H-J—*Nematodirus aspinosus* (H—Ventral view of male tail, setaceous spicules distally fused; I & J—Lateral and ventral view of spicule tips). K—*Murshidia elephasi* (Spicules). L—*Trichuris vulpis* (Tip of cirrus and spicule). M-N—*Habronema* "senrati" (Tips of left and right spicules). O-P—*Cyathostomus ocellatus* (Spicules and gubernaculum). Q-R—*Paracanthocheilus curcui* (Spicules and gubernaculum). S—*Dirofilaria repens* (spicules). T—*Oxoidofilaria* sp. (Spicules). U—*Trichostrongylus probolurus* (Spicules and gubernaculum). V—*Dicheilonema horridum* (Ventral view of male tail, reversed sides). W-X—*Oxyuris equi* (W—Longitudinal section of female rectum; X—Dorsal view of female rectum). Y-Z—*Stenurus minor* (Lateral and ventral views of male tail). AA—*Proleptus obtusus* (Reconstruction of cloacal region of male). BB—*Setaria tundra* (Spicules). CC—*Trichuris vulpis* (Tip of spicule af-

ter exposure to Fairchild's trypsin). DD-EE—*Rhabditis strongyloides* (Spicules, distally fused). FF—*Ostertagia trifida* (Spicules and gubernaculum). GG-MM—*Hyostromylus rubidus* (Serial sections through cloacal region of male showing telamon, gubernaculum, spicules, spicular pouch and cloaca). NN—Various spicular shapes (1, arcuate; 2, hamate; 3, arcuate distally; 4, falcate; 5, setaceous; 6, sigmoid; 7, linear; 8, fusiform; 9, elongate; 10, bent or boomerang shaped; 11, cuneiform; 12, L-shaped). D-E, after Hagmeyer, 1912, Zool. Jahrb., Abt. Syst., v. 32; F, after Senrat 1913, Bull. Soc. Nat. Afrique Nord Alger v. 5; G, U & FF, after Kalantarian, 1928, Trudy Gosudarstv. Inst. Eksper. Moskva, v. 5; H-J, after Rajewska, 1931, Zitsch. Infekt. v. 40; K, after Wu, 1934, Sinensia v. 5; M-N & V, after Skrjabin, 1917, Parasit. v. 9; O-R after de Man, 1889, Mem. Soc. Zool. France, v. 2; W-X, after Martini, 1916, Zitsch. Wiss. Zool. v. 106; Y-Z, after Baylis and Daubney, 1925, Parasit. v. 17; AA, after J. F. Mueller, 1925, J. Parasit. v. 12; BB, after Rajewskaja, 1928, Die Setarien etc.; NN, after Cobb, 1898, Misc. Publ. No. 215, Dept. Agric. N. S. Wales; remainder original.



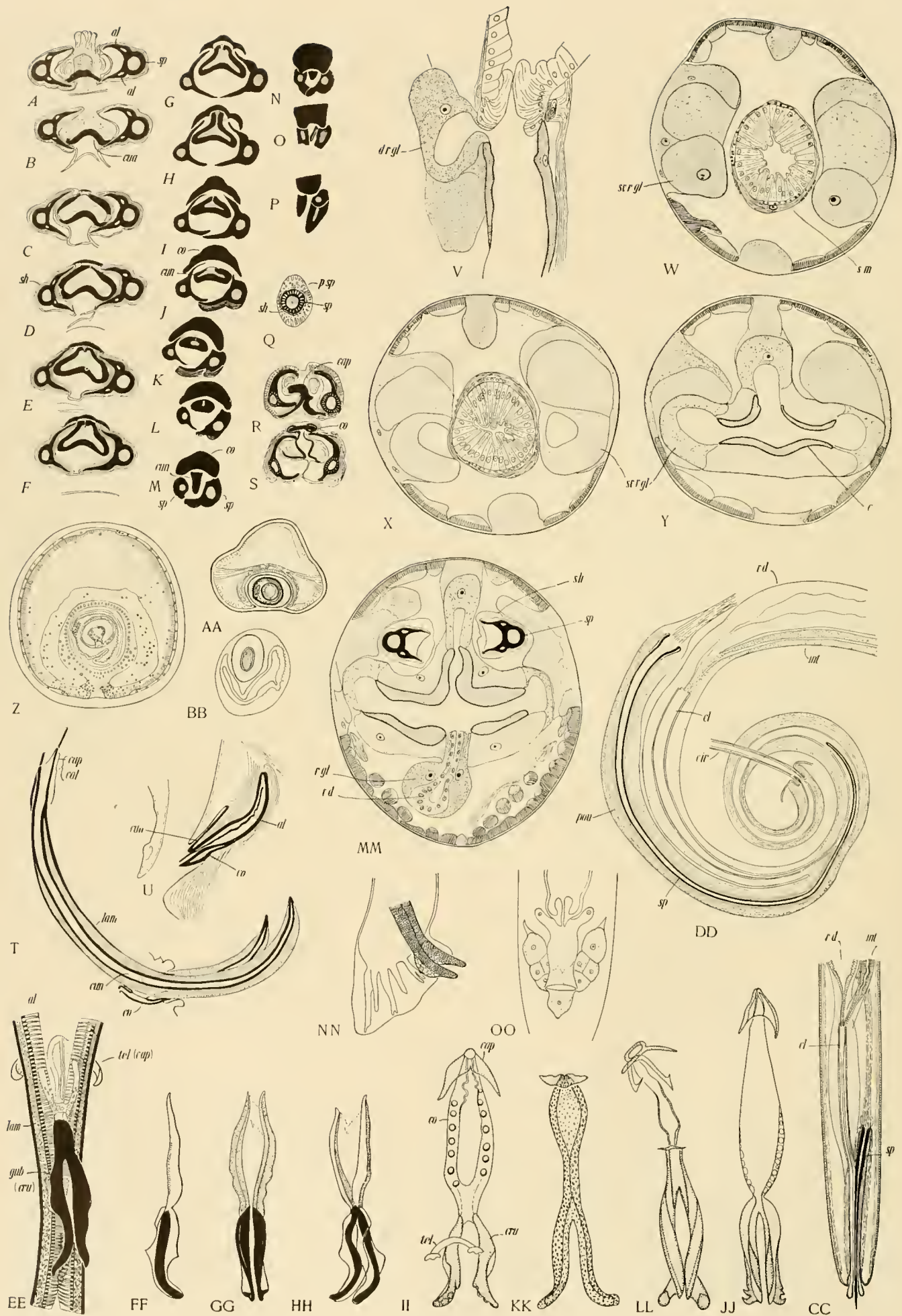


FIG. 110  
118



ier and often terminates in a massive hook (Fig. 109 M, N, T).

While often specific, the form of the spicules sometimes varies and more than one specimen should always be studied. The writers found marked variation in spicular morphology in *Dirofilaria immitis* from an abnormal host (muskkrat). In addition to the normal type, a specimen in which the left spicule blade was degenerate and another in which the left spicule was absent were found in a single muskrat. Such findings cause one to be somewhat dubious of the numerous species of filariids being described at the present time, and differentiated chiefly or wholly on diversity in spicular form.

Differences in spicular morphology of related species may be due to the degree of cephalation, length and differentiation of the shaft, or length and character of the blade. The blade may be highly twisted as in *Dicheilonema* (Fig. 109 V); twisting and irregularity of the blade is particularly characteristic of some genera of the Trichostrongylidae (Fig. B, U, FF). In addition the blade may be distally branched (Fig. 109 A, MM) or the flanges separated from the tube.

The spicules are seldom very long in proportion to the body in free-living nematodes, one of the most outstanding exceptions to this rule being *Metoncholaimus pristiurus* (Fig. 18) in which the spicules are one-twentieth of the body length (seven times as long as the anal body diameter). In parasitic nematodes both the absolute and relative spicule lengths may be many times greater. Thus, Wehr (1933) found the two equal spicules of *Odontospirura cetiopenis* (Spiruridae, Haemaphysomatinae) to attain lengths of 10-11 mm in specimens 15- to 17 mm. Ransom (1904) found the left spicule of *Gongylonema ingluvicola* to attain 17 to 19 mm in specimens 17 to 19 mm long (when retracted it twists and extends through only three-fourths of the body length); in the same form he found the right spicule to be only 0.1 mm long. Seurat (1913) found that the left spicule of *Tetraceros inermis* reaches 1.187 mm in length and the right only 0.075 mm in specimens of a total length of 2.125 mm (Fig. 109 F). Long spicules most commonly occur in representatives of the Spiruroidea, Filarioidea, Dioctophymatoidea, and Trichuroidea and in those forms where the vagina is long and tubular. One might attempt to correlate the length of the vagina with that of the spicules were it not that one finds related species with vaginae of about equal length and spicules relatively much smaller.

#### E. GUBERNACULUM AND TELAMON

The gubernaculum is by common definition a cuticular thickening (sclerotization) of the dorsal wall of the cloaca. This definition is at once misleading. The gubernaculum is formed from the wall of the spicular pouch. Proximally it is usually not in direct contact with the spicular cavity but is to be seen as one or more plates in the wall of the spicular pouch; distally it may come to be the dorsal wall of the pouch or it may project free into the lumen (Fig. 110 U). The cuticle of the gubernaculum, like that of the spicules, is in direct continuation with the pouch lining but unlike the spicules its sclerotized layers may extend beyond this covering internally. The gubernaculum is essentially a plate in the groove of which the spicules move. This condition is seen in many nematodes such as *Rhabditis* (Fig. 49 L), *Ancylostoma*, etc. In others, however, the medial part of the plate may protrude into the spicular pouch separating the spicules. The posterior part of the gubernaculum may then be termed the *corpus* and the anterior (medial) piece, the *euneus*. Where this division occurs the spicules are usually alate. In *Spironoura* (Fig. 110 A-U) the gubernaculum divides near its proximal end giving off an anterior branch (*euneus*) which comes to lie free in the spicular pouch; each dorsal spicular flange thus runs in a groove formed by the *euneus* and *corpus* of the gubernaculum.

Hall (1921) proposed the term *telamon* for an "ornamental supporting structure" formed in the ventral and lateral walls of the cloaca of *Hyostromylylus rubidus* (Fig. 109 C). This structure differs from the gubernaculum and spicules in staining capacity and is more like the external cuticle. As may be seen from section (Fig. 109 GG-MM) Hall's interpretation as to the origin of the *telamon* is correct. It is an immovable sclerotized part of the cloacal wall which apparently serves to turn the spicules posteriorly when they are protruded from the spicular pouch into the cloaca; otherwise the spicules might break through the ventral cloacal wall. Ordinarily such a protective structure would be unnecessary since the spicular pouch orifice is immediately opposite the cloacal opening but in the *Strongylini* this is not the case.

Since Hall's original publication much confusion has resulted from the application of the terms gubernaculum and *telamon*, particularly in the Metastrongylidae. Cameron (1927) used the term *telamon* for lateral protrusible branches (*crura*) of the corpus which he described as "ornamental supporting structures near the cloacal aperture" (Fig. 110 EE-JJ). Gebauer (1932) applied the term *telamon* to a medial ventral sclerotization of the spicular pouch (Fig. 110 EE) (the structure now known as the *capitulum*) and the term gubernaculum to the unpaired and paired subdorsal sclerotizations of the spicular pouch (*corpus* and *crura*). The structures involved have been discussed by Shu'its, Orlov and Kutass (1933), and by Dikmans (1935). A restudy of *Protostrongylus* indicates that the former authors correctly interpreted the entire complex as a gubernaculum. The most important differentiation between gubernaculum and *telamon* is that the *telamon* is formed directly from the cloacal lining while the gubernaculum is formed from the spicular pouch. Though the gubernaculum is primarily dorsal, it is also primarily medial, i. e., it may develop proximal to the union of the spicular pouches and, as in *Spironoura* it may be composed of two or more parts which are heavily sclerotized, these parts being joined by feebly sclerotized regions. Thus the medial (ventral) piece (Fig. 110 RS) termed the *telamon* by Gebauer, is actually a part of the gubernaculum named the *capitulum* by Shu'its, Orlov and Kutass; the two posteriorly directed pieces (*crura*) termed the *telamon* by Cameron and the gubernaculum by Gebauer are joined anteriorly to the *capitulum* by the unpaired piece, *corpus* (Fig. 110 S).

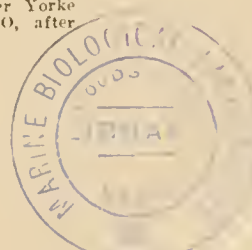
The confusion in terminology has led workers in other groups to misapply the term *telamon*. Thus Steiner and Albin (1933) termed the anterior parts of the gubernaculum (*crura*) of *Deontostoma californicum* (Fig. 37, 4-5) a *telamon*. In so far as the writers are aware, a true *telamon* does not exist outside the *Strongylini*.

The gubernaculum is often complex in free-living nematodes and the various parts are worthy of discussion. De Man (1886) described the gubernaculum of *Enoplus communis* (Figs. 110 A, C-D) as being composed of three parts: an unpaired medial piece (termed *euneus*, projecting anteriorly into the cloacal cavity between the spicules) to which is joined posteriorly and laterally a less sclerotized structure (*corpus*) which in turn has two strongly sclerotized lateral pieces (*crura*). These lateral pieces project into the cloacal cavity on each side of the spicules, each of which moves in a separate groove between *euneus* and *crura*, guided posteriorly by the *corpus*. In other aphasmidians many variations of the above described arrangement are known to occur. In *Acanthonchus viriparus* (Fig. 15 M), and *Paracanthochus caccus* (Fig. 109 Q-R) the ends of the *crura* are dentate while in *Cyatholaimus elongatus* they are denticulate. There is a marked diversity in development of the parts in closely related forms. Thus de Man (1889) found the *crura* to be quite massive and apparently detached (*euneus* and *corpus* absent) in *Paracanthochus caccus* while

Fig. 110

A-P—*Spironoura affine* [Kathliniidae] (Serial cross sections through spicules and gubernaculum). Q-S—*Protostrongylus rupicaprae* [Metastrongylidae] (Q—Cross section of shaft, i. e., calomus, of spicule; R—Cross sections of gubernaculum and blade, i. e., lamina of spicules). T-Y—*Spironoura affine* (T—Spicules and gubernaculum cleared in 10 per cent NaOH; U—Gubernaculum and spicular ala in longitudinal section; V—Intestino-rectal valve and dorsal gland of female, longitudinal section; W-Y—Sections of female through intestino-rectal region showing dorsal and subventral rectal glands and their orifices). Z—*Trichuris suis* (Cross section of male near cloacal opening). AA—*T. trichiura* (Cross section near cloacal opening). BB—*T. suis* (Cross section of cloaca with spicular pouch about to emerge from its walls; according to Rautner more posteriorly the cloacal walls completely surround the spicule forming a double layer). CC—*T. suis* (Reconstruction of male tail; according to Rautner the internal lining of the cirrus is continuous with the cloacal lining anteriorly and is not the lining of the spicular pouch. The upper part of the cloaca has a double lining, the two layers fusing proximally). DD—*T. vulpis* (Tail of male

cleared in phenol). EE—*Protostrongylus austriacus* (Gubernaculum and spicules labelled by Gebauer; correct terminology in parenthesis). FF-HH—*Protostrongylus rupicaprae* (Gubernaculum in various views). II—*P. kochi* (Gubernaculum); JJ—*P. railletii* (Gubernaculum). KK—*P. leuckarti* (Gubernaculum). LL—*Cystocaulus nigrescens* (Gubernaculum). MM—*Spironoura affine* (Cross section of male at junction of rectum and vas deferens showing orifices of dorsal, ordinary subventral and secondary subventral rectal glands; cuticle is absent in region of gland orifice). NN—*Dictyocaulus filaria* (Lateral view of male tail showing spongy type of spicules). OO—*Faleaustera lambdiansis* (Ventral view of rectal region of preadult male showing spicular primordia). Z, BB & CC, after Rautner 1918, Zool. Jahrb., Abt. Anat., v. 40. AA, after Rautner, 1909, Ergeb. u. Fortschr. Zool., v. 1: EE-HH, after Gebauer, 1932, Ztschr. Parasitenk., v. 4; II-LI, after Schulz, Orlov & Kutass, 1933, Zool. Anz., v. 102; NN, after Yorke & Mapleton, 1926, Nematode Parasites of Vertebrates; OO, after Seurat, 1920, Hist. Nat. Nemat. Berberie; remainder original.





in *Cyatholaimus ocellatus* he found the cuneus-corpus (Fig. 109 O-P) extremely large, the crura considerably smaller and in addition he found a small anterior ventral piece (capitulum). In the latter species the spicules are guided anteriorly, posteriorly, medially and laterally. In other forms such as *Syringolaimus striatocaudatus* (Fig. 111 E) and *Anoplostoma viviparum*, de Man (1888, 1907) described well developed grooved crura accompanied by a weak corpus and in these cases each spicule moves in a groove of the corresponding crura. In *Theristus normandica* (Fig. 111 F-G) the gubernaculum appears to surround the spicules, and de Man (1890) found it to be scarcely differentiated into separate parts, but the medial region projects as a cuneus between the spicules and the lateral parts partially surround the spicules and serve as crura. In *Sphaerolaimus hirsutus* (Fig. 111 H-I) the same author found a gubernaculum much like that of *Theristus* but a capitulum in addition. Another type of variation, particularly characteristic of the Axonolaimidae and Linhomoeinae, though sometimes occurring in other groups, is due to the presence of two posterior prolongations of the corpus, termed the *apophyses*. In *Terschellingia longicaudata* the spicules are separated by a distinct cuneus and held in position laterally by flanges of the corpus, no distinct crura being present, while in *Metalinhomoeus typicus* (Fig. 111 J-K) capitulum, cuneus, crura, corpus, and apophyses may all be distinguished.

The musculature of the gubernaculum has been previously described (p. 43) but the origin and insertion of the various muscles is not as limited as previously indicated. The gubernaculum often behaves as though hinged at the junction of the spicular pouch and cloaca. Muscles (protractor gubernaculi) attached to the proximal ends of the gubernacular corpus, crura or the distal ends of the apophyses extend posteriorly to the ventral body wall and their contraction moves the distal ends of the corpus, crura, and cuneus anteriorly, forcing the spicules outward, their tips pushed anteriorly (into the female). Muscles from the proximal ends of the crura in such an instance (*Enoplus*) extend laterally and ventrally to the body wall; their contraction moves the distal ends of the various gubernacular parts posteriorly withdrawing the spicules.

#### FUNCTION OF THE SPICULES

Though it was recognized by Schneider (1866, p. 244) that the spicules are never hollow and that spermatozoa do not ordinarily flow "through them," the conception that they are hollow and act as true intromittent organs has somehow persisted. A locutory and excitatory function has been ascribed to the spicules by Schneider (1866), Bütschli (1872), Rauter (1909, 1918, 1930), Seurat (1920), Baylis (1929), Mueller (1930) and Chitwood & Chitwood (1933). On the other hand, Looss (1905) and zur Strassen (1907) considered that the two flanged spicules in *Ancylostoma* and *Philometra* come together in the form of a tube and that the sperm flows between them. The transmission of sperm down the groove or between the grooves of flanged spicules has been considered probable by Mueller (1925), Baylis (1929) and Rauter (1930). In cases where the spicule or spicules are devoid of flanges, their cross section being practically circular throughout (*Ascaris*, *Trichuris*, *Diectophyma*) there seems to be no conceivable way by which they could "conduct the sperm." Regarding this type of spicule, Mueller (1930) was of the opinion that they are withdrawn during the period of sperm movement for he found a copulating pair of *Ascaris* in which, upon section, the spicules were found not to be inserted. However, observations of copulating nematodes in which the spicules have been seen alternately inserted and withdrawn have been numerous and Mueller's finding seems hardly significant. The spicules take an active part in copulation and we have merely to define that part.

In forms with flanged spicules, do the flanges ever form a tube or groove by which the sperm pass to the female? Tube formation by two spicules in forms such as *Spironoura*, *Ancylostoma* and *Protostrongylus* is undeniable. This tube is formed by the orientation of the spicules by the gubernaculum (Fig. 110 A-T, 33K) while they are still in the spicular pouch. There seems to be no way by which the sperm could gain entrance to this closed tube after it reaches the cloaca.

The spicules might more plausibly play the role of sperm transmitters in forms where the spicules are dissimilar and one of them is flanged or where the spicules are distally fused with a median groove. Mueller (1925) described such an instance in *Proleptus* in which he noted that the blade of the left spicule had wide flanges forming a nearly complete tube open proximally as well as distally. He also found a cloaca-spicular canal connecting the upper part of the cloaca with the spicular pouch just anterior to the beginning of the spicular

blade (Fig. 109 AA). Such a condition has been seen neither before nor since. The writers can more easily think of flanges as primarily for the purpose of increased rigidity and it is conceivable that the flanges aid in keeping an open passage-way into the vaginal lumen.

The movement of the spicules back and forth during copulation would serve not only to keep the vulva and vagina open but also, at least to some extent, would actually propel the sperm into the female.\* Branching of the spicular blade and twisted spicula formation such as occurs in trichostrongyles (Fig. 109 U, FF) would seem to be particularly adapted to such activity. In forms with markedly unequal and dissimilar spicules it is notable that the vagina is always quite long and tubular. Seurat (1920) advanced the view that in such species the short spicule opens the lips of the vulva and the proximal region of the vagina while the long spicule assures the progression of the sperm in the long vagina. It is true that the short spicule usually has a large hook which would be well adapted as a holdfast.

The gubernaculum is, of course, primarily a spicular guide and prevents the spicules from breaking through the wall of the spicular pouch and cloaca when exerted. In such forms as *Terschellingia*, *Enoplus* and *Spironoura* it may also act as a levator. Ordinarily the gubernaculum is not everted during

\*Seurat states that the spicules are absolutely immobile during copulation but in living free-living nematodes such as *Rhabditis* the writers have observed alternate withdrawal and insertion over extended periods.

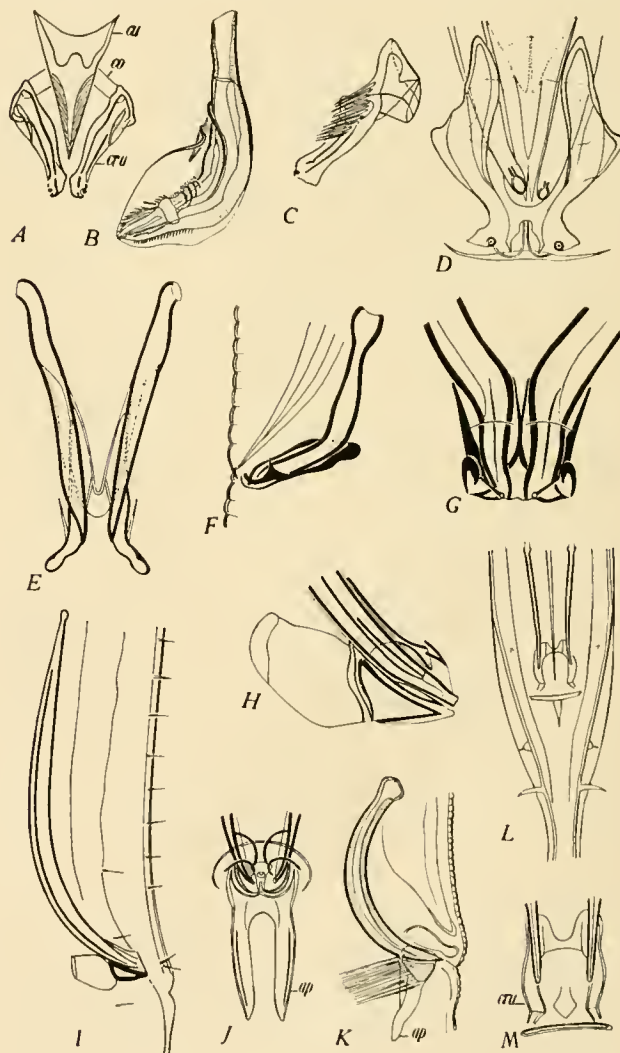


FIG. 111

A-C—*Enoplus communis* (A—Gubernaculum, ventral view; B—spicule; C—gubernaculum). D—*E. brevis* (Gubernaculum and tips of spicules). E—*Syringolaimus striatocaudatus*. F-G—*Theristus normandica* (Spicules and gubernaculum, lateral view, F and ventral view, G). H-I—*Sphaerolaimus hirsutus* (H—Detail of gubernaculum as seen in I). J-K—*Metalinhomoeus typicus* (J—Ventral view; K—lateral view). L-M—*Anoplostoma viviparum* (L—Ventral view; M—detail of gubernaculum). A-D, after de Man, 1886, Nordsee Nematoden; E, after de Man, 1888, Mem. Soc. Zool. France, v. 1; F-G, after de Man, 1890, *Ibid.*, v. 3; H-M, after de Man, 1907, *Ibid.*, v. 20.



copulation but in forms with denticulate or dentate erura such as *Paracanthonehus* and *Cyatholaimus* (Fig. 109 O R) it would seem that they are adapted for gripping the vulvar lips and holding the vulva open.

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## CORRECTIONS FOR PART I

- Page 4, column 1, line 28, 1685 to read 1683.  
 Page 4, column 2, line 13, 1856 a-b to read 1865 a-b.  
 Page 5, column 2, line 55, *derm* to read *Idem*.  
 Page 13, column 1, line 1, of Fig. 12, *Dictyocaulus viviparus* to read *Dictyocaulus viviparus*.  
 Page 13, column 2, line 2-3, of Fig. 12 delete *E* through *Parasit*.  
 Page 19, column 1, line 1, Fig. 18, *Metoncholaimus pristiurus* to read *Metoncholaimus pristiurus*.  
 Page 21, column 1, line 6, *Morpholoige* to read *Morphologie*.  
 Page 22, column 1, line 13, Fig. 23, *Xinema perfectum* to read *Xyala striata*.  
 Page 23, column 2, last line, *Xinema perfectum* to read *Xyala striata*.  
 Page 24, column 1, line 2, Fig. 31, *Ascaridae* to read *Ascarididae*.  
 Page 27, column 2, line 1, Fig. 37, *Stener* to read *Steiner*.  
 Page 32, column 1, line 1, Footnote, *Strongylus equinus* to read *Strongylus equinus*.  
 Page 33, column 2, line 67, *Monographic* to read *Monographie*.  
 Page 42, column 2, line 48, *Dictophymatina* to read *Dioctophymatina*.  
 Page 45, column 2, line 10, *Tcensk* to read *Tetensk*.  
 Page 46, column 2, line 41, *founded* to read *rounded*.  
 Page 49, column 2, line 12, *fungiforous* to read *fungivorous*.  
 Page 50, column 1, line 68, delete *or absent*.  
 Page 51, column 1, line 15, *stome* to read *stoma*.  
 Page 51, column 2, line 23, *Reflexted* to read *reflexed*.  
 Page 51, column 2, line 42, *reflexted* to read *reflexed*.  
 Page 52, column 1, line 1, *Ambulatory* to read *ambulatory*.  
 Page 52, column 1, line 59, *Eurystominac* to read *Eurystomininae*.  
 Page 52, column 2, line 41, *Tetradonematidae* should be bold face type.  
 Page 52, column 2, line 42, *Mermithidae* should be bold face type.  
 Page 53, column 2, *ptr*, *protorhabdian* should read *protorhabdion*.

## ABBREVIATIONS

*al*, ala;  
*an*, anus;  
*ap*, apophysis;  
*cal*, calomus;  
*cap*, capitulum;  
*c gl*, caudal gland;  
*ci*, cirrus;  
*cl*, cloaca;  
*co*, corpus;  
*c m*, copulatory muscle;  
*cru*, crura;  
*cu, cum, cn*, cuneus;  
*d r gl*, dorsal rectal gland;  
*e*, nucleus in esophago-intestinal valve;  
*ep c*, epithelial cell;  
*g*, gland cell nucleus;  
*gub*, gubernaculum;  
*h*, depressor ani;  
*i m*, somato-intestinal muscle;  
*int*, intestine;  
*lam*, lamina;  
*l sp*, left spicule;  
*m*, marginal nucleus;  
*m c*, mesenterial cell;  
*n*, nerve cell nucleus;  
*pou*, spicular pouch;  
*p gub*, protractor muscle of gubernaculum;  
*p sp*, protractor muscle of spicule;  
*r*, radial nucleus;  
*r gl*, rectal gland;  
*r sp*, right spicule;  
*s*, questionable nucleus;  
*sh*, sheath;  
*s m*, sphincter muscle;  
*sp*, spicule;  
*sup or*, supplementary organ;  
*sv r gl*, subventral rectal gland;  
*tcl*, telamon;  
*v d*, vas deferens;  
*x*, questionable nucleus.







